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ABSTRACT

This module is part of a series designed to be used by life science students for instruction in the application of physical theory to ecosystem operation. Most modules contain computer programs which are built around a particular application of a physical process. This module describes heat transfer processes involved in the exchange of heat between an organism and its environment. Emphasis is placed on conduction, convection, and evaporation, three of the physical processes that affect the physiological, behavioral, and ecological activities of all organisms. Radiation transfer is described in a separate module. Four examples taken from the ecological literature are used to emphasize the biological effects of temperature and energy budgets. Three systems are used to illustrate heat transfer principles and their biological importance. These include heat flow in soil, a leaf, and a lizard. Ecological examples are used throughout the text and problem set. Calculus and first-year physics are prerequisites for the module. (Author/CS)

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PHYSICAL PROCESSES IN TERRESTRIAL AND AQUATIC ECOSYSTEMS

TRANSPOPT PROCESSES

HEAT TRANSFER PROCESSES FOR THE THERMAL ENERGY BALANCE OF ORGANISMS

by

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University of Washington

SE 034 164

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R.D. Stevenson

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PREFACE

The way in which an organism exchanges heat with its environment explains several characteristics of its behavior and its preferred habitat. This module presents a thorough introduction to heat transfer processes and assumes the reader has a background in calculus and first-year physics. Emphasis is placed on conduction, convection and evaporation. Radiation transfer is described in its own module. Ecological examples are used throughout the text and the problem set.

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INTRODUCTION

The purpose of this module is to further elucidate the physics of the heat transfer processes: radiation, evaporation, conduction, and convection. An understanding of these processes and their interactions will provide a clearer ecological interpretation of the thermal energy environment. Two ideas need to be recalled about the First Law of Thermodynamics (Zemansky and Van Ness 1966, Stevenson 1979*a*): first, that the heat energy budget is based on the conservation principle of the First Law, and second, that this law can be applied to any system of arbitrary boundaries. Although organisms seem a natural choice, Collins et al. (1971) have found the nasal passageway to be a useful system for study of nasal vapor recovery. In a previous module (Stevenson 1979*b*), we considered a stream, a leaf, and a spider as well-defined thermodynamic systems for understanding the biological importance of heat fluxes.

Before we begin to describe the mechanisms of heat transfer, four examples are taken from the ecological literature to emphasize the biological effects of temperature and energy budgets. As the examples are presented, the reader should ask, "How does the thermal environment influence the distribution, abundance, and life history strategies of the organism being described?"

Boylen and Brock (1973) have studied the benthic algae of the Firehole River in Yellowstone National Park. They were interested in documenting the effects of the heated water entering the river from geysers. The Firehole was coldest during June when the discharge was largest from the snowmelt. Diatoms in the genera *Nitzchia, Synedra, Rhopalodia, Cocconeis,* and *Comphonema* were present at the sampling

stations with cooler water temperatures, while green algae, *Spirogyra*, *Oedogonium*, *Cladophora*, and *Stigeoclonium*, were dominant at the warmer stations. Biomass was 15 times larger and growth rates five times greater in the heated than the unheated section of the river. Boylen and Brock feel that the Firehole River represents a unique opportunity to study the biological consequences of elevated water temperature which are similar to the increases caused by power plants.

The acquisition of nutrients is of fundamental importance to plants. Chapman (1974) studied the absorption of phosphate along thermal gradients, where: 1) the average soil temperature changed and the variability was constant; and 2) where the mean was the same but the fluctuation or variability was changing. The maximum rate of phosphate absorption was found to correlate well with the mean soil temperature for each species. He found that cold-adapted species also increased the root-to-shoot ratio presumably in order to compensate for the slower absorption rates at colder temperatures. Species from fluctuating environments showed a greater rate of acclimation to phosphate absorption than did species from more constant environments. These results suggest that plants from different environments try to maintain similar phosphate uptake rates, which is accomplished with different physiological adaptations, and that plants can partition their energy resources (root and shoot biomass) to achieve this balance.

Our third example concerns temperature adaptations in amphibians. Snyder and Weathers (1975) hypothesized that the variability tolerated in body temperatures of amphibian species would be correlated with the variability in air temperatures. To test this idea, the difference

between the maximum and lower lethal body temperature for 11 species was taken from the literature and plotted against the difference in the high and low mean monthly air temperatures for a 10-yr period. Figure 1 presents their results and is consistent with their hypothesis.

Several authors (Schneirla et al. 1954, Scherba 1960, Jackson 1957) have investigated the effects of microclimate on ant activity and nest structure. Nest and bivouac temperatures are important for egg, larva and pupa development. Golley and Gentry (1964) found that soil surface temperature was an important factor influencing the activity of the Florida harvester ants. Figure 2 shows that *Pogonomyrmex badius* was not active in June and July when the soil surface became very hot during midday hours. Also there was little activity in February, when soil surface temperatures were cold. Carlson and Gentry (1973) further found that continual shading of this species' entry holes causes a large increase in the migration of colonies to new nest sites. Sunshine is probably an important energy contribution needed to raise the ant's body and gallery temperatures.

It is sometimes useful to take a more general outlook. In that spirit, here are six ecological questions which could be more easily interpreted and answered with a sound knowledge of heat transfer physics:

1) Does the climate limit the geographical distribution of an organism?

2) What selective advantage is there to being a particular color, shape, or size?

3) What microhabitats are available throughout the day to maintain a thermal balance?

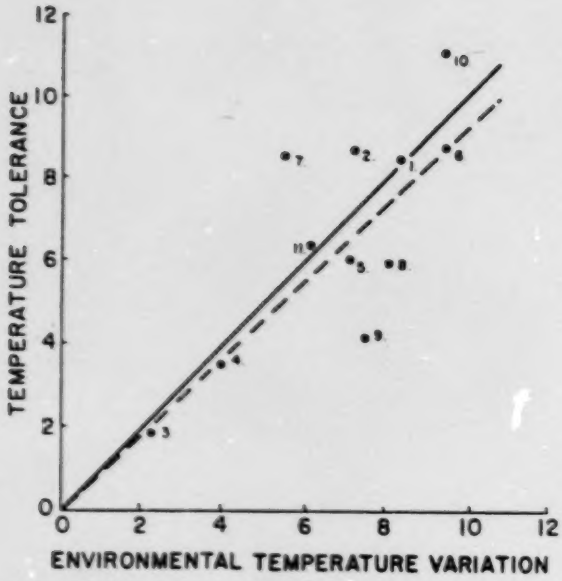


Figure 1. The relation of increase in range of temperature tolerance and increase in environmental temperature variation (see text for methods of determining these values). The continuous line is a line of equality relating increase in temperature tolerance and environmental temperature variation. The dashed line has been fitted to the data with the method of least squares. The numbers indicate the species included. These are: 1) *Bufo alvarius*, 2) *B. debilis*, 3) *B. marinus*, 4)*B. marmoreus*, 5) *B. mazatlanensis*, 6) *Hyla regilla*, 7)*H. smithi*, 8) *Leptodactylus melanolus*, 9)*Pternohyla fodiens*, 10) *Scaphiopus hammondi*, 11) *Smilisca baudini*. (From Snyder, G.K. and W.W. Weathers, 1975, p. 98).

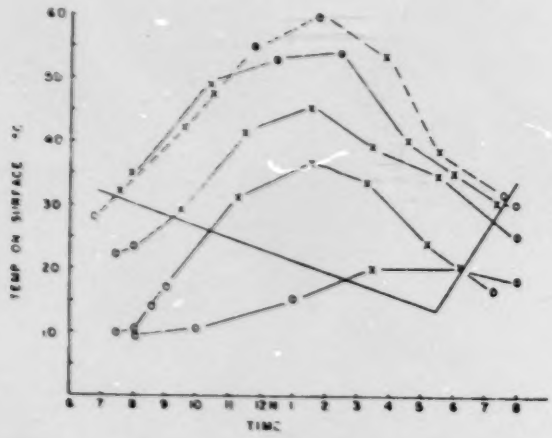


Figure 2. Surface activity of *Pogonomyrmex badius* in relation to temperature of the ground surface and time of day. Active ants on the mound are indicated by crosses; inactive mounds are indicated by open circles; half-closed circles denote very slight activity. The months represented, beginning with the highest curve at 12 noon, are June, July, May, October and February. (From Golley, F.B. and J.B. Gentry, 1964, p. 224.)

4) Is there a daily activity pattern that limits prey-predator interactions or foraging time?

5) What selective advantage is there to be a poikilotherm or homeotherm?

6) How does the thermal balance affect photosynthetic and transpiration rate of a plant?

The reader should be cautioned that there are other ecological factors such as competition, predation, and coevolution, which may be greater selective influences and which may interact with selective pressures of the physical environment. Predictions from models incorporating physical processes can often be tested quantitatively which allows the investigator to compare the importance of the physical process under consideration with other ecological factors.

HEAT TRANSFER PROCESSES

Radiation

Radiation is a process of energy transfer that requires no intervening medium. The dual nature of radiation, its particle (photon) and wavelike properties have important biological consequences. All matter radiates energy as individual photons (Kreith 1973) but for heat transfer problems the wavelike description is more useful. This is because energy at different wavelengths interacts with matter in different ways (but *see* Problem 2). Figure 3 shows the different wavelengths of electromagnetic spectrum.

Since radiation travels at the speed of light c_L, the product of the frequency f and the wavelength λ is a constant:

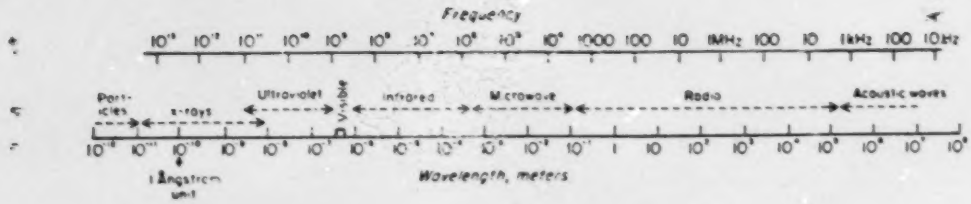


Figure 3. The electromagnetic spectrum. (From Byers, H.R., 1974, p. 8).

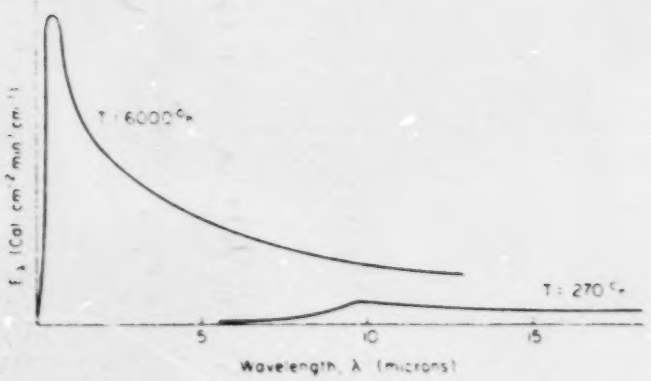


Figure 4. Schematic representation of blackbody emission spectra, as a function of wavelength, for temperatures of 6000 and 270 K. (From Lowry, W.P., 1969, p. 17.)

$$c_L = f\lambda. \qquad (1)$$

All objects, living and nonliving, radiate thermal energy. The amount and kind (wavelength in the electromagnetic spectrum) of energy depend on the temperature and physical characteristics of the radiating body. Figure 4 shows the energy radiated by the sun and the earth as a function of wavelength. It should be clear from the figure that the portion of the electromagnetic spectrum radiating from the sun occurs at much shorter wavelengths than that of the earth. In fact, the sun's peak radiation on a wavelength plot is in the green part of the visible spectrum, while the earth's radiation is completely in the infrared region.

Three physical laws are associated with Fig. 4. Planck's Law gives the energy emitted, E_λ, as a function of the wavelength, λ, if the temperature of the radiating body is known:

$$E_\lambda = c_1\lambda^{-5}\,[\exp(c_2/\lambda T) - 1]^{-1} \qquad (2)$$

where

E_λ is the amount of energy emitted in the band λ to $\lambda + d\lambda$ (J m^{-1}),

T is the blackbody temperature (K),

λ is the wavelength (m),

c_1 is $2\pi h c_L^2$,

c_2 is hc_L/K_b,

where

h is Planck's constant = 6.63×10^{-34} (J s),

K_b is Boltzmann's constant = 1.38×10^{-23} (J K^{-1}),

and

c_L is the speed of light = 3.00×10^{8} (m s^{-1}).

It is obvious that no one has actually measured the surface temperature of the sun. In this instance, the sun's temperature was deduced from its electromagnetic spectrum. Second, from Planck's Law, it can be demonstrated (Robinson 1966 or Roseman 1978) that the wavelength at the maximum radiated energy is only a function of the temperature of the radiating body.

$$\lambda_{max} = \frac{2.897}{T} \times 10^{-3}, \qquad (3)$$

where

λ_{max} = wavelength of maximum radiation (m),

and

T = temperature (K).

Third, the Stefan-Boltzmann Law provides the even more remarkable result that the total energy emitted, Q_e, by a radiating body (the area under the curve (Fig. 4)) is proportional to the fourth power of the surface temperature T_s.

$$Q_e = \varepsilon\sigma(273 + T_s)^4, \qquad (4)$$

where

Q_e is the radiant energy emitted from the surface ($W\ m^{-2}$),

ε is the emissivity (range zero to one),

σ is the Stephan-Boltzmann constant ($5.67 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$, 8.17×10^{-11} cal $min^{-1} cm^{-2} K^{-4}$),

and

T_s is the surface temperature (°C).

Roseman (1978) gives a more complete discussion of these laws.

Kirchoff studied the emissivity and absorptivity of materials. He showed that the energy absorbed at any specific wavelength λ at constant temperature is equal to the energy emitted at λ. That is, if the absorptivity of a surface $a(\lambda)$ represents the fraction of incident radiation absorped at λ and $\varepsilon(\lambda)$ is the emissivity, the radiation emitted at λ divided by the radiation emitted from a blackbody, then $a(\lambda) = \varepsilon(\lambda)$ for each wavelength. If $\varepsilon = 1$ for all wavelengths, then the object is said to be a blackbody. Although no system is a perfect blackbody, many are approximately so. In the infrared region, 3 to 100 μm, most objects such as vegetation, soil and water behave like blackbodies ($\varepsilon = 1$). Table 1 gives the emissivities of some plants and animals.

This, however, is not true in the visible part of the spectrum. In general, any wavelength can be absorbed, reflected, or transmitted. This is written:

$$a(\lambda) + r(\lambda) + t(\lambda) = 1 \qquad (5)$$

Table 1. Long Wave Emissivities (from Monteith, J.L., 1973, p. 68.)

LEAVES	
Species	Average
Maize *(Zea mays)*	94.4 ± 0.4
Tobacco *(Nicotiana tabacum)*	97.2 ± 0.6
Snap bean *(Phaseolus vulgaris)*	93.8 ± 0.8
Cotton *(Gossypium hirsutum Deltapine)*	96.4 ± 0.7
Sugar cane *(Saccharum officinarum)*	99.5 ± 0.4
Poplar *(Populus fremontii)*	97.7 ± 0.4
Geranium *(Pelargonium domesticum)*	99.2 ± 0.2
Cactus *(Opuntia rufida)*	97.7 ± 0.2

ANIMALS			
Species	Dorsal	Ventral	Average
Red squirrel *(Tamiasciurus hudsonicus)*	95-98	97-100	
Gray squirrel *(Sciurus carolinensis)*	99	99	
Mole *(Scalopus aquaticus)*	97	--	
Deer mouse *(Peromyscus sp.)*	--	94	
Grey wolf			99
Caribou			100
Snowshoe hare			99
Man *(Homo sapiens)*			98

Table 2. Reflectivities of Biological Materials for Solar Radiation (from Monteith, J.L., 1973, pp. 66-67.)

LEAVES
Reflection coefficients r (%) for Solar Radiation

Species	Upper	Lower	Average
Maize *(Zea mays)*			29
Tobacco *(Nicotiana tabacum)*			29
Cucumber *(Cucumis sativa)*			31
Tomato *(Lycopersicon esculentum)*			28
Birch *(Betula alba)*	30	33	32
Aspen *(Populus tremuloides)*	32	36	34
Oak *(Quercus alba)*	28	33	30
Elm *(Ulmus rubra)*	24	31	28

Table 2. (Cont'd.)

VEGETATION -- MAXIMUM GROUND COVER

Farm Crops	Daily Mean	Farm Crops	Daily Mean
Grass	24	Wheat	22
Sugar beet	26	Pasture	25
Barley	23	Barley	26
Wheat	26	Pineapple	15
Beans	24	Sorghum	20
Maize	18 - 22	Sugar cane	15
Tobacco	19 - 24	Cotton	21
Cucumber	26	Groundnuts	17
Tomato	23		
Natural Vegetation	**Daily Mean**	**Natural Vegetation**	**Daily Mean**
Heather	14	Natural pasture	25
Bracken	24	Derived savanna	15
Gorse	18	Guinea savanna	19
Maquis, evergreen scrub	21		
Forests and Orchards	**Daily Mean**	**Forests and Orchards**	**Daily Mean**
Deciduous woodland	18	Eucalyptus	19
Coniferous woodland	16	Tropical rainforest	13
Orange orchard	16	Swamp forest	12
Aleppo pine	17		

ANIMAL COATS

Mammals		Dorsal	Ventral	Average
Red squirrel *(Tamiasciurus hudsonicus)*		27	22	25
Gray Squirrel *(Sciurus carolinensis)*		22	39	31
Field mouse *(Microtus pennsylvanicus)*		11	17	14
Shrew *(Sorex sp.)*		19	26	23
Mole *(Scalopus aquaticus)*		19	19	19
Gray fox *(Urocyon cinereo argentus)*				34
Zulu cattle				51
Red Sussex cattle				17
Aberdeen Angus cattle				11
Sheep weathered fleece				26
Newly shorn fleece				42
Man *(Homo sapiens)*	Eurasian			35
	Negroid			18
Birds		**Wing**	**Breast**	**Average**
Cardinal *(Richmondena cardinalis)*		23	40	
Bluebird		27	34	
Tree swallow		24	57	
Magpie		19	46	
Canada goose		15	35	
Mallard duck		24	36	
Mourning dove		30	39	
Starling *(Sturnus vulgaris)*				34
Glaucous-winged gull *(Larus glaucescens)*				52

where

$a(\lambda)$ = absorptivity at wavelength λ,

$r(\lambda)$ = reflectivity at wavelength λ,

$t(\lambda)$ = transitivity at wavelength λ,

and each term is between zero and one (*see* Siegel and Howell 1972 for a more complete discussion). Table 2 gives some values for r averaged over the entire spectrum for different ecological systems. Values of a, r, t are also given by Porter (1967) for animals and Monteith (1973) for plants and animals.

As an example of radiation flux, let us calculate the radiant energy emitted by the cactus, *Opuntia rufida*. To do this, we must specify the emissivity ε and the surface temperature T_s. In Table 1, $\varepsilon = .977$ for *O. rufida* and, if we take $T_s = 10\ ^{o}C$, then:

$$Q_e = .977 \times 5.67 \times 10^{-8} (10 + 273)^4 = 355.5\ W\ m^{-2}. \qquad (6)$$

If we wish to know the total heat loss per second and (1 watt = 1 J s^{-1}) the plant, we must multiply our answer by the surface area of the cactus.

The calculation of absorbed radiation Q_a, although straightforward with some assumptions, is a lengthy task because several longwave and shortwave components must be included. Gates and Stevenson (1979) have devoted an entire module to this topic to which the interested reader should refer for additional information.

Conduction

Conduction, G, describes the physical process of molecular thermal energy flow within a solid, fluid or gas. In fluids and especially gases, motion of the medium usually makes the process of convection a more important mechanism of heat transfer than conduction. Heat flows by conduction when nearby molecules have more internal energy (higher temperature) and thus a greater mean kinetic energy. Energy can be transferred by molecular collisions (fluids) or by diffusion (solids) (Kreith 1973, pages 4-5).

In conduction, the rate of heat flow depends on the thermal conductivity of the material, the area through which the heat flows and the temperature gradient in the material. Equation (7) describes the relation as:

$$G = -kA_c\frac{dT}{dx} \qquad (7)$$

where

G is conduction (W),

k is thermal conductivity (W m^{-1} $^oC^{-1}$),

A_c is the area through which the heat is flowing (m^2),

and

$\frac{dT}{dx}$ is the thermal gradient (^oC m^{-1}).

The negative sign in equation (7) is to indicate that the direction of heat flow is from regions of higher temperature to lower temperature (opposite the temperature gradient). This is shown in Fig. 5.

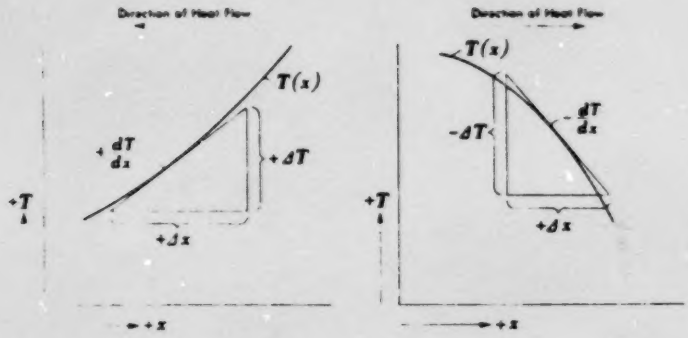


Fig. 5. Sketch illustrating sign convention for conduction heat flow. From Kreith, F. 1973. P. 8.

The thermal conductivity depends on the molecular structure of the material. Some cooking pots have copper-coated bottoms because this metal transfers heat better than other materials. Home insulation materials reduce the flow of heat because they trap air which has a low thermal conductivity. The hollow centers of the hair shafts of some mammals reduces the conduction of heat along the fiber. The thermal conductivity can be calculated by measuring the heat flow when the temperature slope (Fig. 5) is one.

As an example of conduction, we will examine the heat flow between the alligator, *Alligator mississippiensis*, and substratum. We assume that the skin is the same temperature as the ground and that the animal is in good thermal contact with the surface (there are no air pockets reducing heat flow). The conduction exchange can now be calculated as follows: The thermal conductivity of fat is 0.20 W m^{-1} $^oC^{-1}$ while soil-rock range of conductivity is between 0.556 and 3.25 W m^{-1} $^oC^{-1}$. Since the fat layer of 0.7 cm has a lower conductivity, it controls the rate of heat flow. Here we also assume that 0.5 m^2 of the alligator at T_b = 22 ^oC are in contact with the ground at T_g = 30 ^oC. In steady state, the conductive

heat flux is then a linear function of the potential, as given in equation (7).

$$G = \frac{kA_c}{x}(T_b - T_g) = \frac{.198 \times 0.5}{0.007}\ (22-30) = -114\ W, \qquad (8)$$

where

G is conduction (W, negative since energy is flowing from the ground to the animal),

T_b is body temperature of the alligator (°C),

k is the thermal conductivity of fat ($W\ m^{-1}\ {}^{o}C^{-1}$),

T_g is ground temperature (°C),

and

Δx is thickness of layer (m).

Before proceeding to a discussion of convection, it is important to talk about an alternative view of conduction. It is possible to rewrite equation (8) as

$$G = K_g(T_b - T_g). \qquad (9)$$

The rate of heat flow is then equal to a conductance K_g times a potential, the temperature difference. The conductivity, area of contact and length have all been subsumed into K_g. When working heat transfer problems, it is also common to speak and think of resistances to heat transfer. A resistance is simply the reciprocal of the conductance. If there is a large resistance to heat flow, there is a low conductance. Monteith (1973) and Campbell (1977) have adopted the resistance approach for describing mass and momentum fluxes as well as heat transport. This concept originated with Ohm's Law where the electrical current flow is

equal to the potential or voltage drop divided by the resistance of the material. Thus, the correspondence of a flux driven by a potential is called Ohm's Law analogy. Kreith (1973, chapters 1 and 2) shows how radiation, convection and evaporation can also be thought of in these terms. It should be remembered though that in general the Ohm's Law analogy, due to the complications introduced by turbulent mass and turbulent energy transfer, is an approximation (*see* Tennekes and Lumley 1973).

Conduction is often ignored in the heat transfer of plants and animals because one must know or make assumptions about the temperatures, boundary layer thickness, thermal conductivity, and contact resistance. There are not many actual measurements reported in the ecological literature but Mount (1968), Derby and Gates (1966), Gatesby (1977), and Thockelson and Maxwell (1974) offer some interesting examples of the importance of conduction.

Convection

"Convection" is the transfer of heat between solids and fluids (i.e., gases and liquids) or when fluids of different temperatures are in contact. Conduction takes place with nearby particles on the molecular level but the additional factor of the circulation of the fluid distinguishes convection from conduction. When there is no motion in the fluid except that caused by density gradients and by the resultant buoyant forces, this process is called "free convection." If the fluid is moving relative to the other fluid or solid, the process is called "forced convection." If the flow is turbulent, besides the molecular processes,

there will be increased heat transfer caused by the bulk transport of fluid. Also, at certain fluid velocities, free and forced convection may both contribute to the convection term. Indeed convection is comprised of several complex physical processes occurring simultaneously.

Water and air are the two fluids that commonly interest the thermobiologist. Most aquatic organisms are at ambient water temperature; hence, convective transfer is unimportant because there is no temperature difference. Marine mammals, birds, a few large fish and turtles, however, maintain body temperatures above water temperature, which requires thick insulation (Bartholomew 1977, Schmidt-Nielsen 1975). This is because the high specific heat (4.18×10^3 J kg^{-1} $^oC^{-1}$) and thermal conductivity (59.8 W m^{-2} $^oC^{-1}$) of water create a large heat loss. The extra heat transferred due to the movement of the fluid has not been examined for many organisms (but *see* Eskine and Spotila 1977 and Lueke et al. 1976). Although the specific heat and thermal conductivity of air are much less than for water, convection is still a significant mode of heat transfer for terrestrial organisms.

As with conduction, convective heat flow can be thought of as a potential (the difference in temperature between the surface of the object and the surrounding fluid) times a conductance. The conductance is most commonly written as the product of two terms as in equation (10):

$$C = h_c A_c (T_s - T), \qquad (10)$$

where

C is the convective heat flux (W),

h_c is the convective heat transfer coefficient (W m^{-2} $^oC^{-1}$),

A_c is the area at object in contact with the fluid (m^2),

T_s is the surface temperature of the object (^oC),

and

T is the fluid temperature (^oC).

Usually, A_c, T_s and T can be evaluated. (One particular problem, however, is the surface temperature of a furry object. Kowalski (1978) has shown that in this case it is best to define the system boundary at a solid surface where a temperature can be measured.) The heat transfer coefficient, on the other hand, is often a difficult parameter to estimate in the natural environment because of turbulence (Kowalski and Mitchell 1976, and Noble 1975). Generally, it is established as follows:

$$h_c = \frac{Nu\ k}{D} \qquad (11)$$

where

h_c is the heat transfer coefficient ($W\ m^{-2}\ ^oC^{-1}$),

Nu is the Nusselt number,

k is the thermal conductivity of the fluid ($W\ m^{-1}\ ^oC$),

and

D is the characteristic dimension of the system (m).

The heat transfer coefficient, h_c, is a value which has been averaged over the entire surface area of the system. The characteristic dimension D must be defined for each different geometric shape one wishes to consider. Commonly, one might use the diameter of a sphere or the widest point of a leaf in the direction of the wind. The Nusselt modulus is a

nondimensional number used to scale laboratory results to other wind velocity and fluid properties. Kreith (1973, page 317) gives two physical interpretations for the Nusselt number. It may be thought of "as the ratio of the temperature gradient in the fluid immediately in contact with the surface to a reference temperature gradient $(T_s - T)/D$" or the "ratio D/x where x is the fluid thickness of a hypothetical layer which, if completely stagnant, offers the same thermal resistance to the flow of heat as the actual boundary layer."

In practice, another nondimensional number, the Reynolds number, Re, which is the ratio of inertial (ρv^2) to viscous forces ($\mu V/D$), is introduced to account for the scaling effects of fluid velocity, geometry, and fluid properties (*see* Kreith 1973 or Cowan 1977 for a discussion of Re).

$$Re = \frac{\rho V D}{\mu} \qquad (12)$$

where

ρ is the fluid density (kg m^{-3}),

V is the fluid velocity (m s^{-1}),

D is the characteristic dimension (m),

and

μ is the fluid viscosity (kg m^{-1} s^{-1}).*

For a particular geometry, a functional relationship between the Nusselt number and the Reynolds number can then be calculated from laboratory

* Sometimes the kinematic viscosity ν (m^2 s^{-1}) is used in the Reynolds number where $\nu = \mu/\rho$.

measurements (h_c versus V). Usually, the result is expressed as:

$$Nu = a\ Re^b \tag{13}$$

where a and b are determined by regression. The parameters will be different for different shaped objects (Kreith 1973), then, using equation (12), the Nu can be calculated which in turn will yield the convection coefficient from equation (11). This procedure is the standard method used in engineering. In ecological studies, where one is concerned about the effects of wind speed and size and the geometry of the system is constant, the convection coefficient is sometimes given without specifically indicating the coefficient of equation (13) as in the following example. This approach is more direct and is fine to use as long as the student realizes what has been implied.

Tibbals et al. (1964), from earlier experimental work by Gates and Benedict (1963), were able to use the following formula to evaluate convective exchange for a leaf:

$$C = k_1 \left(\frac{V}{D}\right)^{0.5} (T_s - T_a) \tag{14}$$

where

C is the convective heat flux ($W\ m^{-2}$, positive for heat flow from the leaf to the air),

k_1 is 9.14 ($J\ m^{-2}\ {}^oC^{-1}\ s^{-1/2}$),

V is wind velocity ($m\ s^{-1}$),

D is the characteristic dimension (widest point) of the leaf in the direction of the wind (m),

T_s is the surface temperature of the leaf (°C),

and

T_a is the air temperature (°C).

After using this convection term C in the energy budget equation, Tibbals et al. (1964, page 538) concluded for similar energy environments "that . . . that the broad deciduous type leaf would be considerably warmer than the conifers . . ." and " . . . that the demand on transpiration is probably greatest per unit surface area for the broad-leaf plant than the conifers." (Also *see* Gates 1977.)

The theory of convective transfer is more complex than presented here. Although some additional material will be included in the problems, the reader may wish to refer to Kreith (1973), Monteith (1973) or Campbell (1977).

Evaporation

Evaporation is the process of water changing from a liquid to a gas. For animals, water can be lost through respiration, through special glands, or through any part of the skin. Water loss is usually a small component of the heat balance for animals but may be large for animals with moist skins. It usually increases quickly at higher temperatures. Figure 6 from Dawson and Templeton (1963), shows this effect for the collared lizard, *Crotaphytus collaris*. In general, the water loss, E, is given by equation (15). Again, this is in the form of a potential divided by a resistance (an Ohm's Law analogy).

$$E = \frac{C_o - C_a}{r_e} \qquad (15)$$

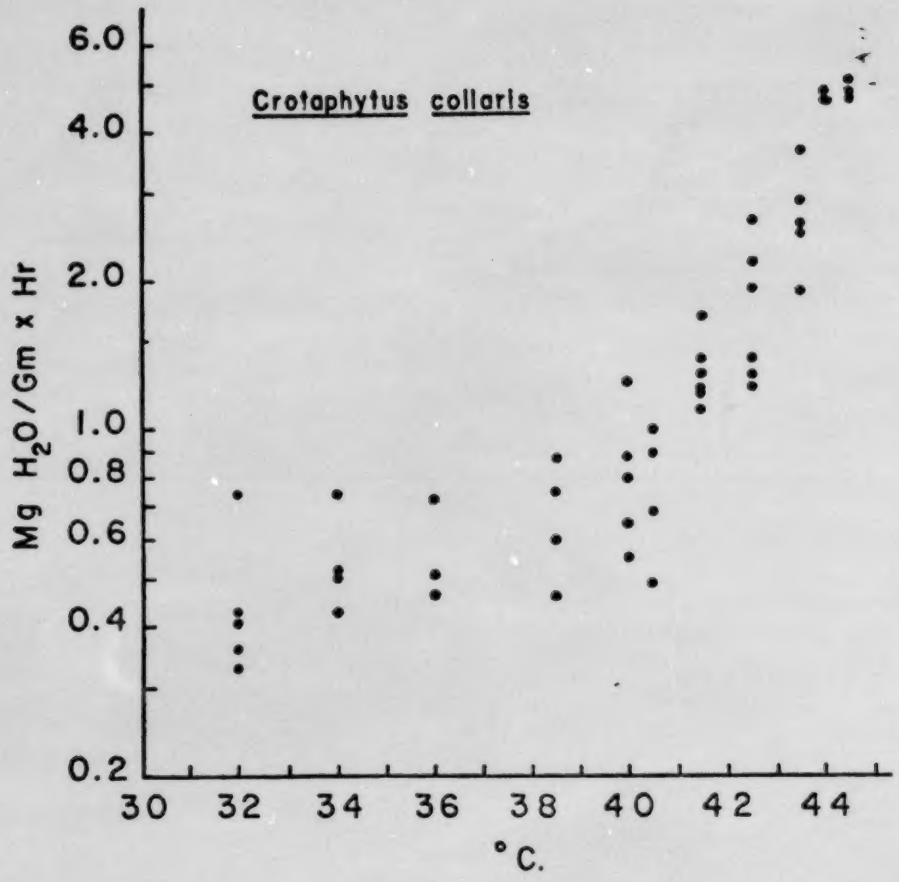


Figure 6. Relation of evaporative water loss to ambient temperature in collared lizards weighing 25-35 g. Data represent minimal values at various temperatures for animals studied. (From Dawson, W.R., and J.R. Templeton. 1963. P. 231.)

where

E is water loss ($kg\ s^{-1}$),

$C_o - C_a$ is the water vapor concentration difference between the surface (o) and the free atmosphere (a) ($kg\ m^{-1}$),

r_e is the resistance to water vapor loss ($s\ m^{-1}$).

The water vapor concentration at the surface of the water loss site may be saturated such as that of a leaf or a lung of a bird but it may be less than saturated as in the skin of a lizard. The concentration in the air is equal to the saturated concentration (at air temperature T_a) times the relative humidity. The resistance to water loss in the skin of a lizard will be controlled by the resistance to water movement in the skin and the boundary layer resistance. In a leaf, the total resistance to water loss is a combination of the stomatal resistance and the boundary layer resistance. But the water loss resistance from the moist skin of a frog was assumed to be equal to the boundary layer resistance only (Tracy 1976). In general, the boundary layer resistance is a function of the diffusion coefficient of water vapor in air and the boundary layer thickness. This thickness in turn depends on the size of the object as well as the wind speed.

To relate the water transport calculated in equation (15) to the energy balance, the mass flux E must be multiplied by the latent heat of evaporation L. L can be closely approximated as a function of temperature.*

$$L(T) = 2.50 \times 10^6 - 2.38\ 10^3\ T, \qquad (16)$$

* L is also a function of pressure. *See* Zemansky and Van Ness 1966.

where

L(T) is the latent heat of evaporation (J kg^{-1}),

and

T is the surface temperature at the site of evaporation (^{o}C).

As an example of the energy flux, the water loss at T_a = 40 ^{o}C for *C. collaris* is 0.8 mg of H_2O g^{-1} hr^{-1} (Fig. 7). Correcting the units to kg s^{-1} for a 30 g lizard yields 6.67 x 10^{-9} kg s^{-1}. Therefore, using equation (16), the energy loss for the animal is 1.6 x 10^{-2} W. In this example, we have not calculated E explicitly, mechanistically accounting for wind speed or water vapor concentration of the environment, but animal physiologists often report evaporation as a function of air or body temperature only. These factors become more important when water loss is a larger fraction of the total energy budget or when one is concerned with the water balance of the organism (Welsh and Tracy 1977). Later in the text, a functional relationship to include these factors is given for water loss from a leaf. Generally, transpiration is a significant energy loss for plants which has led Monteith (1973) to make the distinction between "wet" and "dry" systems.

THERMAL PROPERTIES OF MATERIALS

In the above examples, we have mentioned several thermal properties such as thermal capacity and specific heat. Now we wish to define them more carefully.

Specific heat is defined as:

$$c = \frac{\Delta Q}{\Delta T\, M}, \qquad (17)$$

29

where

c is the specific heat (J kg^{-1} $^oC^{-1}$),

ΔQ is the heat flux (J),

ΔT is a 1^o change temperature (^oC),

and

M is a 1 kilogram system (kg).

We cannot measure the amount of heat a body can hold, so in a sense the term specific heat is misleading, but it is commonly used. It is simply the amount of heat which must be added per unit mass of material for a 1^o rise in temperature. What actually is changing is the internal energy of the system. Table 3 (after Monteith 1973) shows values of specific heat for different materials. See Stevenson (1979a) or Zemansky and Van Ness (1966) for a more formal definition.

The heat capacity of the system can then be obtained by multiplying the mass of the system by specific heat:

$$C = Mc. \qquad (18)$$

For instance, if we consider 0.12 kg of granite and the same weight of peat soil as two systems (*see* Table 3), the heat capacity of each is the specific heat c times the mass M or 96 J $^oC^{-1}$ for granite and 226 J $^oC^{-1}$ the peat. To calculate the energy necessary to raise each system 10 °C, we can employ equation (18) in the form

$$\Delta Q = \Delta T\ M\ c.$$

The answer is found to 960 J for the granite and 2,200 J for the peat.

Table 3. Thermal properties of natural materials.

(From Monteith 1973)

MATERIAL	DENSITY	SPECIFIC HEAT	THERMAL CONDUCTIVITY	THERMAL CAPACITY	THERMAL DIFFUSIVITY
	ρ kg m^{-3} x 10^3	c J kg^{-1} $°C^{-1}$ x 10^3	k W m^{-1} $°C^{-1}$	$c_v = \rho c$ J m^{-3} $°C^{-1}$ x 10^6	$\kappa = \frac{k}{\rho c}$ $m^2 s^{-1}$ x 10^{-6}
Granite	2.60	0.8	4.61	2.08	2.22
Quartz	2.66	0.8	8.80	2.13	4.14
Clay minerals	2.65	0.9	2.92	2.39	1.22
Ice	0.9	2.1	2.30	1.89	1.22
Old snow	0.5	2.1	0.29	1.05	0.28
New snow	0.1	2.1	0.08	0.21	0.38
Wet sand	1.6	1.3	1.68	2.08	0.81
Dry sand	1.4	0.8	0.17	1.12	0.15
Wet marsh soil	0.9	3.4	0.84	3.06	0.27
Peat soil	0.3	1.8	0.06	0.54	0.11
Still water	1.0	4.18	0.63	4.18	0.15
Still air	0.001	1.0	0.02	0.001	20.0
Organic matter	1.30	1.92	0.25		1.00
Fur	0.98		0.33		
Mean body	0.98-1.05	3.42			
Fat		1.88	0.14-0.20		
Plant leaf					
Wood	0.6	1.3	0.15	.78	0.19

An equally valid way of considering the heat capacity of a system is to define the thermal capacity. It is the heat added per degree change per unit volume and thus is equal to the specific heat times the density of the material of the system (*see* Table 3).

$$c_v = \frac{\Delta Q}{\Delta T\ V} \tag{19}$$

where

c_v is thermal capacity (J $^oC^{-1}$ m^{-3}),

ΔQ is the heat change in the system (J),

ΔT is change in temperature (^oC),

and

V is unit volume (m^3).

This is an especially useful concept if we wish to compare systems of equal volume. Let us reconsider our previous example of granite and peat except that now each system will have the same volume of 1.2 m^3. Thus, they are not the same systems as before. The volumetric heat capacity for each is the product of the thermal capacity and the volume which for granite turns out to be 2.5×10^6 J $^oC^{-1}$ and for peat 0.65×10^6 J $^oC^{-1}$. We have found an increase in the heat capacity for the second granite system and a decrease in the heat capacity in the second peat system. This result is expected if we consider the densities of each material.

Thermal conductivity along with the notions of conductance and thermal resistance have already been discussed and defined in the section on conduction. The last parameter we wish to define is the thermal

diffusivity κ which is the ratio of the thermal conductivity κ divided by density ρ times the specific heat.

$$\kappa = \frac{k}{\rho c} \left(\frac{J\ m^{-1}\ {}^{o}C^{-1}\ s^{-1}}{kg\ m^{-3} J\ kg^{-1}\ {}^{o}C^{-1}} \right)$$

$$= m^2\ s^{-1}. \qquad (20)$$

The thermal diffusity is important in nonsteady state conduction problems where thermal energy can be stored or transported as shown in the first example of heat flow in the soil.

EXAMPLES OF THE HEAT ENERGY BUDGET

To illustrate the heat transfer principles and their biological importance, we chose three systems: the soil, a leaf, and a lizard. Again, the reader is asked to think of the ecological importance of the system and how the thermal balance influences physiological processes as the examples are presented.

Heat Flow in Soil

In soil, heat flow has great biological importance. Not only does the energy balance control the soil temperature, but it greatly affects the moisture content. Both factors are important for photosynthesis in green plants. Soil temperature also influences nutrient uptake as we have seen in our example at the beginning of the module. Fungi, bacteria, insects, as well as many other invertebrates and vertebrates, commonly spend part or all of their life cycles in or surrounded by the soil. Soil temperatures influence metabolic rates and may serve as a behavioral cue for daily and seasonal activity patterns.

The simplest representation of heat flow in the soil is a conduction process where the heat flux dQ per unit time dt is equal to the conductivity k times the difference in temperature dT over a unit path length dz.

$$\frac{dQ}{dt} = -k\frac{dT}{dz}. \tag{21}$$

The minus sign is used to indicate that the potential gradient is in the direction of decreasing temperature.

Another result can be derived by considering Fig. 7. The First Law states that the change in internal energy (storage) is equal to the inflow minus the outflow. The change in internal energy will be equal to the mass (ρdz) times the heat capacity (c), multiplied by the change in temperature with time (ΔT).

$$c\rho\Delta T\ dz = k\left(\frac{dT}{dz}\right)_U - k\left(\frac{dT}{dz}\right)_L$$

$$\Delta T = \frac{k}{c\rho}\frac{1}{dz}\left(\left(\frac{dT}{dz}\right)_U - \left(\frac{dT}{dz}\right)_L\right)$$

$$\frac{\partial T}{\partial t} = \frac{k}{c\rho}\frac{\partial^2 T}{\partial z^2}. \tag{22}$$

Equation 22 is a form of the diffusion equation and $\frac{k}{c\rho}$ is called the thermal diffusivity. This equation can be solved analytically if simple enough boundary conditions are assumed and the thermal diffusivity remains constant. In general, the diffusivity is a function of the water content of the soil and the soil temperature (here numerical methods must be used). We can, however, get a feeling for the heat transfer profile by noting the general boundary conditions. We know that at the soil surface under steady state conditions the temperature will cycle daily while at some depth z_o below the surface the temperature will not change.

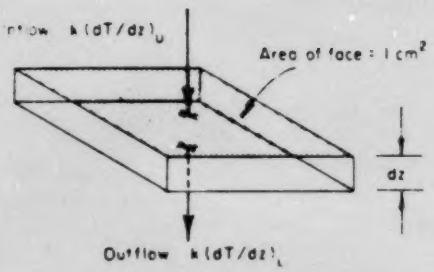


Figure 7. Schematic view of a unit of soil, showing heat inflow from above and heat outflow below, leading to derivation of Eq. 22. (From Lowry, W.P. 1969. P. 51)

Figures 8 and 9 from Lowry (1969) give different representations of how the soil might change with time and depth. Simpson (1977), Carslaw and Jaeger (1959), and Van Wijk (1966) present a more detailed discussion of soil heat flow.

A Leaf

Our second example is the energy balance of a leaf. Gates (1968) chose to model the heat balance of a leaf because it has a distinct physical geometry and because it is the unit of photosynthesis. The governing heat flux equation for the steady state condition was given in the module on the First Law of Thermodynamics and is repeated here:

$$Q_a = Q_e + C + LE, \tag{23}$$

where

Q_a is the radiant energy absorbed by the leaf ($W\ m^{-2}$),

Q_e is the energy emitted by the leaf ($W\ m^{-2}$),

C is the convective flux ($W\ m^{-2}$),

and

LE is the evaporative flux ($W\ m^{-2}$).

With empirical measurements and some assumptions (*see* Gates 1977), equation (23) is expanded as:

$$Q_a = \varepsilon\sigma(T_\ell + 273)^4 + k_1\left(\frac{V}{D}\right)^{0.5}(T_\ell - T_a) + L(T_\ell)\,\frac{C_o(T_\ell) - \text{r.h.}\ C_a(T_a)}{r_\ell + k_2(D^{0.3}\,W^{0.20})/V^{0.50}} \tag{24}$$

where

σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$),

ε is the emissivity of the leaf,

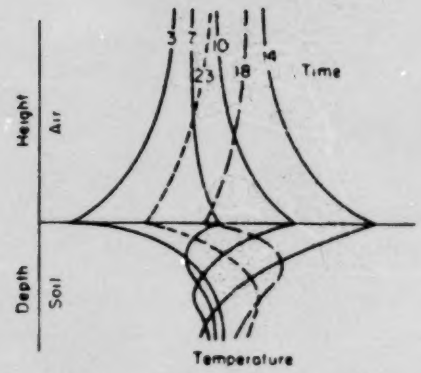


Figure 8. Generalized soil-air temperature profiles (tautochrones) near the soil surface, for four-hour intervals during a diurnal period. (From Lowry, W.P. 1969. P.37.)

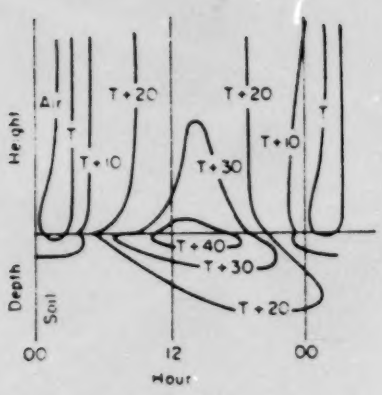


Figure 9. Generalized diurnal patterns of isotherms near the soil surface on coordinates of time and distance. (From Lowry, W.P. 1969. P. 37.)

T_ℓ is the leaf temperature (°C),

V is the wind speed (m s^{-1}),

k_1 is an experimentally determined coefficient (9.14 J m^{-2} $s^{-0.5}$ $°C^{-1}$),

k_2 is an experimentally determined coefficient (183 $s^{-0.5}$ m^{-1}),

T_a is the air temperature (°C),

D is the leaf dimension in the direction of the wind (m),

r.h. is the relative humidity,

W is the leaf dimension transverse to the wind (m),

$C_o(T_\ell)$ is the concentration of water vapor saturation at leaf temperature T_ℓ (kg m^{-1}),

$C_a(T_a)$ is the concentration of water vapor in free air saturated at air temperature T_a (kg m^{-1}),

and

r_ℓ is the internal diffusion resistance of the leaf (s m^{-1}).

Inspection of equation (24) shows that the energy balance of the leaf is very dependent on leaf temperature which in turn affects convection and transpiration. To analyze this multivariate problem, Gates graphed three variables while holding the rest constant. Figures 10 and 11 illustrate thermodynamic conditions that would be common in tropical habitats at midday sunny (Q_a = 1.2 cal cm^{-2} min) and cloudy (Q_a = 0.8 cal cm^{-2} min) radiation levels. Note the differences in transpiration rates and leaf temperatures as a function of leaf resistance. Gates (1968) also considered the effects of leaf size. Figure 12 clearly shows that small leaves, by reducing leaf temperature and transpiration, would be advantageous in desert regions.

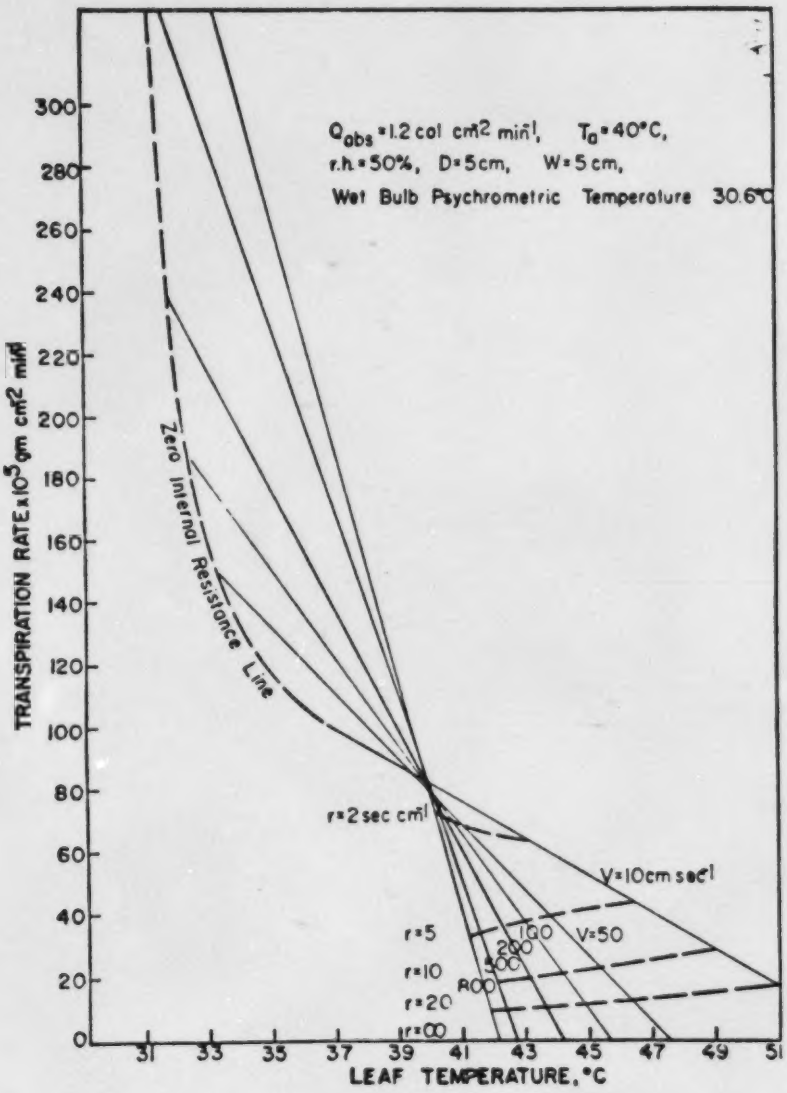


Figure 10. Computed transpiration rate versus leaf temperature as a function of wind speed and internal diffusive resistance for the conditions indicated.
(From Gates, D. M. 1968. P. 216.)

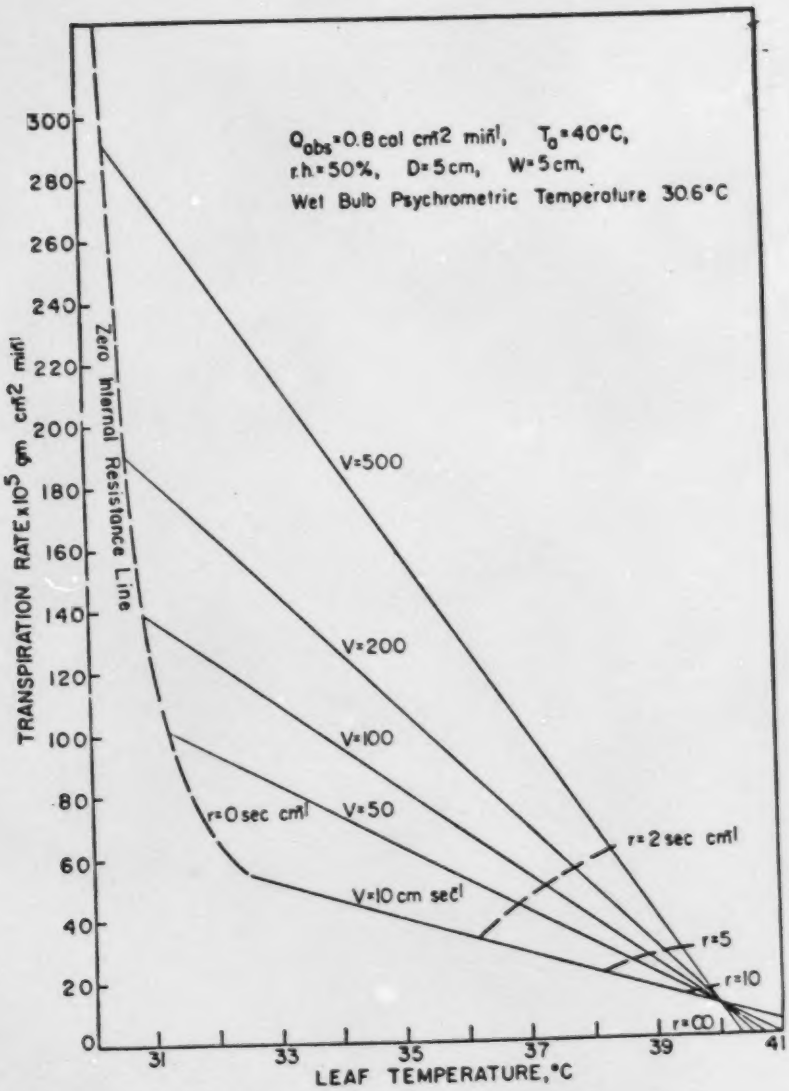


Figure 11. Computed transpiration rate versus leaf temperature as a function of wind speed and internal diffusive resistance for the conditions indicated.
(From Gates, D. M. 1968. P. 217.)

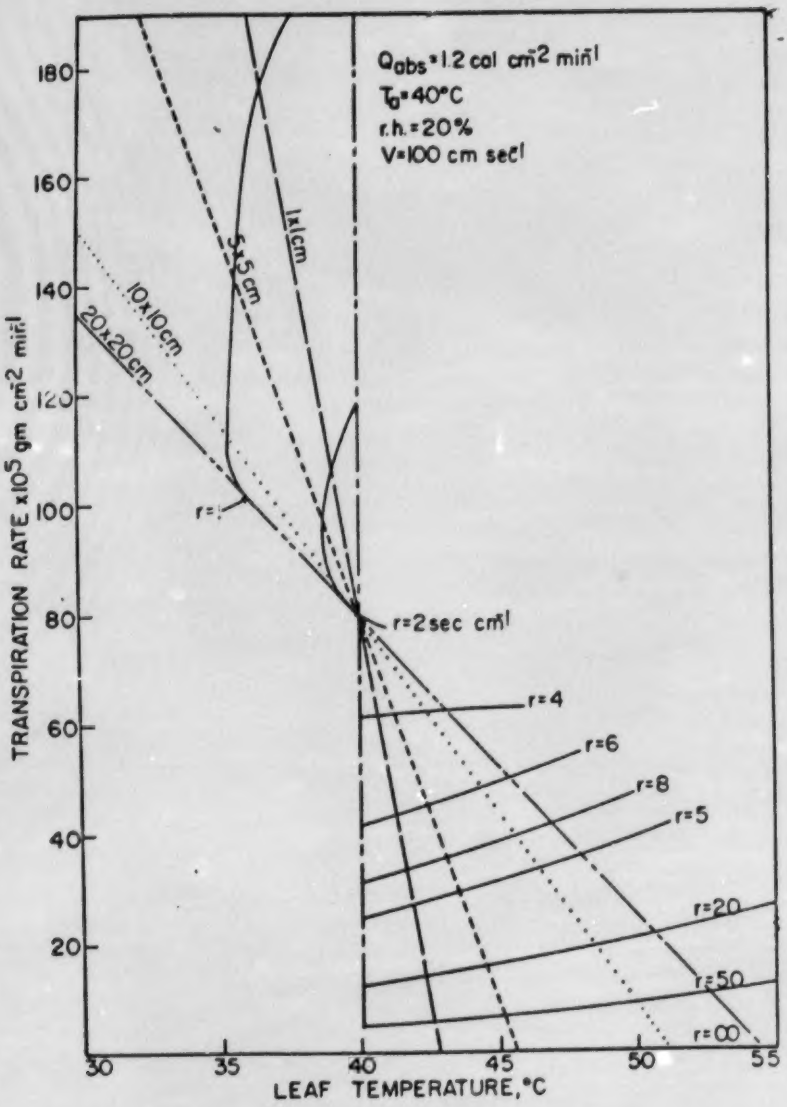


Figure 12. Computed transpiration rate versus leaf temperature for various leaf dimensions and internal diffusive resistances for the conditions indicated.
(From Gates, D. M. 1968. P. 229.)

A Lizard

As a final example, we will review the work of Bartlett and Gates (1967) who computed the heat energy budget for the Western fence lizard, *Sceloporus occidentalis*, on a tree trunk. They hypothesized that *S. occidentalis* oriented itself on the tree trunk so as to maintain its body temperature relatively high and constant. The daily temperature variation of the tree surfaces supported their idea (Fig. 13). The heat energy equation for equilibrium is

$$Q_a + M - Q_e - LE - C - G = 0 \qquad (25)$$

where

Q_a is energy absorbed (W m^{-2}),

M is metabolism (W m^{-2}),

Q_e is radiation emitted (W m^{-2}),

LE is evaporation (W m^{-2}),

C is convection (W m^{-2}),

and

G is conduction (W m^{-2}).

Equation (25) may be rewritten:

$$Q_a + M - \varepsilon \sigma A_e (273 + T_s)^4 - LE - h_c A_c (T_s - T_a) - kA_c \frac{dT}{dx} = 0 \qquad (26)$$

where

ε is emissivity to longwave radiation,

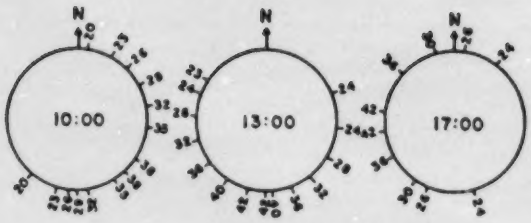


Figure 13. Tree surface temperature in °C on Chew's Ridge at 10:00, 13:00, and 17:00 Pacific Standard Time June 21 as a function of direction from North.
(From Bartlett, P. N. and D. M. Gates. 1967. P. 320.)

σ is Stefan-Boltzmann constant (5.67×10^{-8} W $m^{-2}K^{-4}$),

A_e is the percent of the total surface area of the animal not in contact with substratum,

T_s is surface temperature of the lizard (^oC),

h_c is convection coefficient (W m^{-2} $^oC^{-1}$),

T_a is air temperature (^oC),

k is thermal conductivity of substratum (W m^{-1} $^oC^{-1}$),

A_c is the percent area of the animal total surface area in contact with the substratum,

$\frac{dT}{dx}$ is temperature gradient with the substrate (^oC m^{-1}).

The terms of equation (26) were either experimentally determined or taken from the literature. It was then solved for a variety of situations to obtain a range of values for the animal's energy balance:

1. A maximum heat gain: If the lizard's surface temperature T_s equaled 29.3 ^oC and the lizard was in close contact with the tree.

2. A minimum heat gain: If T_s = 39.9 ^oC and the lizard was not in contact with the tree.

3. Maximum heat loss of T_s= 38.9 ^oC, wind speed = 2.23 m s^{-1} (5 mph) and the animal was oriented at 90^o to the direction of the wind.

4. Minimum heat loss if T_s = 29.3 ^oC, and wind speed was 0.1 m s^{-1}.

5. Intermediate heat loss if T_s = 34.1 ^oC and wind speed = 0.45 m s^{-1}.

Figure 14 gives sample results.

Finally, they calculated the energy losses and gains every hour at 45^o increments around the tree. Using the criterion that the energy losses must fall between the energy gains (Fig. 14), they could predict

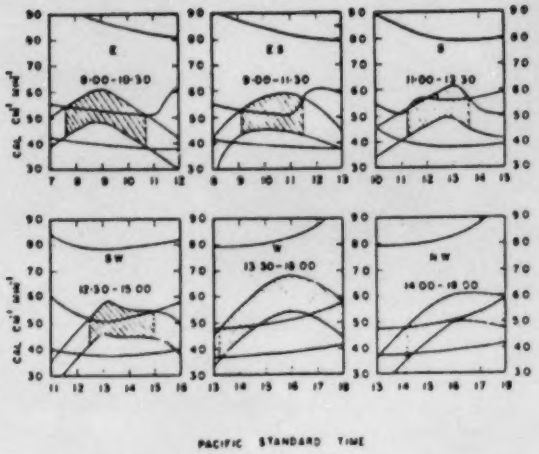


Figure 14. Max and min energy gains (concave downward) and maximum, minimum, and estimated energy losses (concave upward) of a lizard on a tree trunk on Chew's Ridge for selected times and positions on June 21, with times when lizards could be expected to be found at the selected positions. Areas hatched represent times when the estimated energy loss falls between maximum and minimum energy gains. (From Bartlett, P. N. and D. M. Gates. 1967. P. 321.)

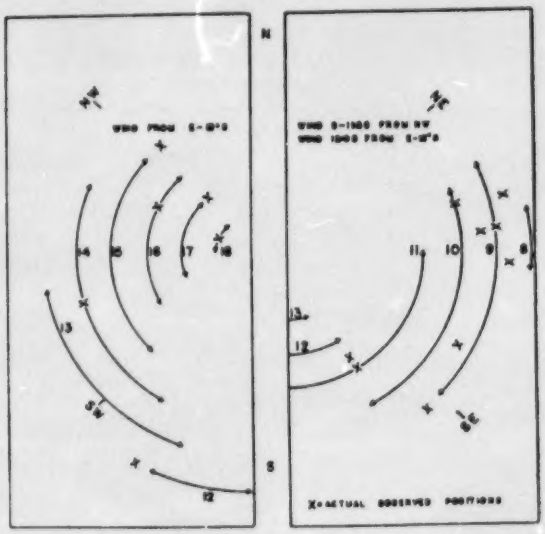


Figure 15. Estimated hourly positions on a tree trunk on Chew's Ridge for June 21 where *Sceloporus occidentalis* could maintain its characteristic body temperature (arrows) and actual observed positions of lizards on June 21, 1964 (crosses). (From Bartlett, P. N. and D. M. Gates. 1967. P. 321 .)

the position of the lizard on the tree trunk as a function of time of day. The predicted and observed positions of the lizards are compared in Fig. 15.

This module has attempted to develop the aspects of heat transfer that are important to biology. Emphasis has been placed on the physical processes, radiation, evaporation, conduction and convection, that influence the physiological, behavioral and ecological activities of all organisms. The discussion in conjunction with the modules on the First Law of Thermodynamics presents the basic physical laws that are needed to describe the heat energy balance of ecological systems.

PROBLEMS

1a. To measure the oxygen consumption of resting homeotherms as a function of the thermal environment, animals are commonly placed in an environmental chamber where the air temperature can be changed and monitored. The results of the experiment are given as a plot of O_2 consumption versus air temperature. Imagine that for some reason the wall temperature is not equal to the air temperature. Plot the radiation emitted by the wall per unit surface area, Q_{ew}, as a function of wall temperature using Stefan-Boltzmann's Law (assume emissivity equals 0.96).

1b. If the emissivity of an environmental chamber with plastic walls is 0.96 for longwave radiation what is its absorptivity to longwave radiation? Imagine that the air is much cooler than the animal's surface. The radiation leaving the animal, incident on the walls, could heat the walls above the air temperature and increase the radiation incidence on the animal. Name two ways to avoid this problem. A chamber with metal walls will have a small emissivity ($\sim$.15) to longwave radiation. What will be its reflectivity? What will happen to the radiation leaving the animal in this case? How can this effect be minimized?

2a. It is also possible to represent Planck's Law as a function of frequency f rather than wavelength λ:

$$E_f = \frac{2\pi h}{C_L^2} \; f^3 \left[\exp\left(\frac{hf}{K_b T}\right) - 1 \right]^{-1}.$$

Equation (1) of the text gives the relationship between λ and f. Show how E_f and E_λ are related. What is the difference in dimensions between E_f and E_λ? The concept of wave number is often introduced to plot E_f and E_λ of the

same graph. Wave number $n = \lambda^{-1}$. How are f and n related? Plot E_λ and E_f for T = 280 K as a function of λ. Repeat for T = 6,000 K but show both the λ and n scales. How does the relationship of bandwidth/ wave number and bandwidth/wavelength change over the spectrum?

2b. Planck also found that the energy in a photon, e, is proportional to its frequency (e = hf). What does this imply for a E_λ versus E_f representation? At what wavelength does the sun radiate the most energy? Assume its surface temperature is 6,000 K. How does this value compare with that in Fig. 4?

3a. Using equation (8), plot the heat of vaporization as a function of temperature. Schmidt-Nielsen (1975, page 313) says that 580 cal g^{-1} is a commonly used value in physiology. Is this a good approximation? Evaluate the error over the range 0 to 40 °C.

b. Schmidt-Nielsen (1975, page 37) gives the lung volume for mammals as a function of weight as

$V = 0.0567\ M^{1.02}$.

V is lung volume (liters) and M is body mass (kg).

If respiration rate (breaths min^{-1}) is a function of air temperature (for a moose (Belovsky 1978)),

$Br = 7.72 \exp(.07\ T_a)$,

calculate the respiration loss in watts as a function of air temperature (T_a = -20 to 40 °C). Assume M = 358 kg, that the exhaled air is at air temperature, the relative humidity is 50 percent and L is constant at 2.43×10^6 J kg^{-1}. Repeat the calculation for the exhaled air at $\frac{T_a + T_b}{2}$.

Hint: The energy lost is equal to the net mass flow (the mass of water exhaled minus the mass of water inhaled per unit time multiplied by the latent heat of water). Convert the volume exchange to a mass exchange using the fact that concentration (mass/volume) of water is the product of the molecular weight, the vapor pressure of water at that temperature and the relative humidity divided by the product of the gas constant and the absolute temperature of the sample.

4. The rate of heat transfer by conduction depends on the potential (temperature difference), the area of contact and the conductivity of the material. Estimate the heat transfer between an animal and the ground for all combinations.

Surface temperature = 20 °C

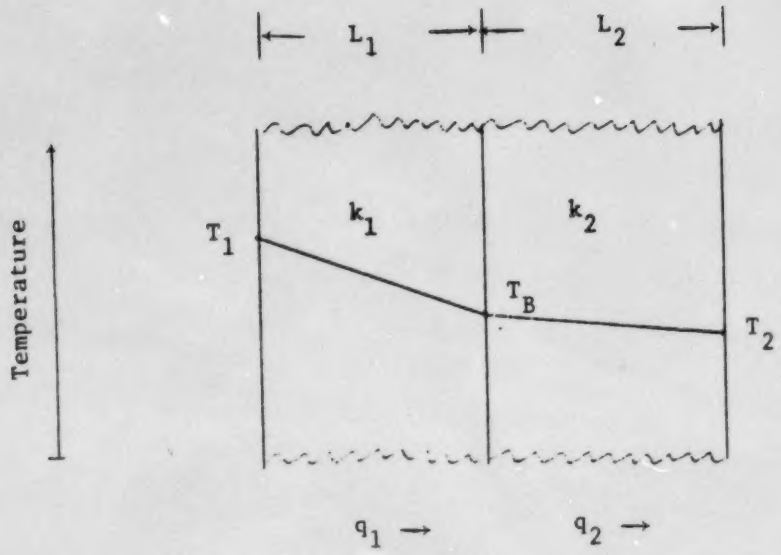
Ground temperatures = 2, 14, 27 °C

Area of contact = 0.054 m^2

Thermal conductivities = 0.02, 0.08, 0.17 W m^{-1} $^oC^{-1}$

Thickness of the material layer limiting heat flow = 0.005 m

5a. In the diagram, heat flows through two materials from the left boundary (temperature T_1) to the right boundary (temperature T_2). Assume steady state conditions.



How does the temperature drop at the boundary depend on thermal conductivity and the thickness of the material? Let $\frac{k_1}{k_2} = a$ and $\frac{L_1}{L_2} = b$; find T_B. Let $\frac{a}{b}$ and find T_B. Plot $\frac{T_B - T_2}{T_1 - T_2}$. If a = 1.2, b = 0.2, T_1 = 40 °C and T_2 = 10 °C, in which material is the temperature gradient larger? Which material has the larger temperature drop? What is T_B?

b. In the conduction section of the text the heat flow between an alligator and the substrate was calculated. It was assumed that the heat flow into the rock was not important. Discuss this assumption with regard to part "a" of this problem.

c. Imagine that the alligator's skin temperature is initially equal to the body temperature. How will the temperature profile change in the soil and in the animal as the heat exchange approaches a constant value?

6. Kreith (1973) gives the following relationship for Nu and Re of cylinders:

$Nu = a\ Re^b$

Re	a	b
0.4-4	0.891	0.330
4-40	0.821	0.385
40-4,000	0.615	0.466
4,000-40,000	0.174	0.618
40,000-400,000	0.0239	0.805

Assume that wind velocity is 2 m s^{-1} and 0.1 m s^{-1}, the diameter is .46 m and .002 m. Compute h_c for the four combinations of diameter and wind velocity. Take $\nu = 1.42 \times 10^{-5}$ m^2 s^{-1} and $k = 2.50 \times 10^{-2}$ W m^{-1} K^{-1} at an air temperature of 10 °C.

7a. Calculate the heat transfer coefficient for a flat plate using $Nu = 0.60\ Re^{0.5}$ (Monteith 1973, page 224; Kreith 1973, page 341). Let air temperature be 20 °C, so $\nu = 1.51 \times 10^{-5}$ m^2 s^{-1} and $k = 2.53 \times 10^{-2}$ W m^{-1} K^{-1}. How does this compare with the convection coefficient for the leaf? This is accurate for laminar flow $Re < 2 \times 10^4$.

b. Show the region $Re < 2 \times 10^4$ on a graph of wind velocity V versus the characteristic length D. When $Re < 2 \times 10^4$, Monteith suggests $0.032\ Re^{0.8}$. How likely is this to occur naturally? Would a leaf be rigid in these wind speeds?

8. In the text, we discussed the physical process of free convection. To determine the importance of free convection, one must compute the ratio of the Grashof number to the square of the Reynolds number. If the ratio is approximately 1, then free convection cannot be ignored. The Grashof number is

$$Gr = \frac{agD^3(T_s - T)}{\nu^2}$$

g = gravitational acceleration (9.8 m s^{-2}),

a = coefficient of thermal expansion for fluid (a = 1/273 for air),

T_s = surface temperature (°C),

T = fluid temperature (°C)

ν = kinematic viscosity (m^2 s^{-1}).

Plot $\frac{Gr}{Re^2}$ on a graph of V versus D. Let $T_s - T$ equal 10, 20 and 30. Below the line $Gr = Re^2$, free convection loss cannot be ignored. Is free convection important for leaves in the natural environment?

9a. The energy balance for fruits is important in both cultivated and wild plants because it affects when and at what rate the crop ripens. Grapes for instance must be picked at just the right time to insure the best sugar content for winemaking. McIntosh apples need cold nights and warm days to be of the best quality. When weather conditions are unfavorable, fruit can become overripe or rotten before it is harvested. Wild plant fruits are an energy investment by the plant to attract seed dispersers. This is especially true of birds and bats in the tropics. The color of the fruit is often an important signal to a potential disperser while the size and spacing of the fruits will influence the animal's harvesting rates. These same characteristics are important to the fruit's thermal balance.

An empirical approach based on the "heat unit" or "growing degree day" concept has been developed to predict the harvest times. When the fruits have been exposed to x degree days the theory says they will be ready to pick. Degree days are computed as follows:

$$DD = \Sigma\left[\frac{T_{amax} - T_{amin}}{2} - T_t\right]$$

where DD is degree days, T_{amax} is the maximum air temperature during the day, T_{amin} is the minimum air temperature for the day and T_t is a threshold temperature specific for each species and which can be thought of as the temperature below which development is stopped. (The summation is over only positive values of the term). From the data below calculate the ripening degree days if T_t is 16 °C.

Day	1	2	3	4	5	6	7	8	9	10
T_{amax} °C	20	25	21	21	18	20	25	27	26	23
T_{amin} °C	16	18	14	13	10	12	15	18	18	16

What problems are there with this approach?

b. A more mechanistic viewpoint should allow one to calculate the temperature of the fruit. As an example let us consider a spherical model 1, 4 and 10 cm in diameter. What is the heat energy balance for the fruit. Which terms are small and can be ignored? What terms are you unsure about? As a first approximation, let us start with the following model:

$$Q_a = Q_e + C,$$

where

Q_a is absorbed radiation (W m^{-2}),

Q_e is reradiation (W m^{-2}),

and

C is convection (W m^{-2}).

Under steady state conditions the temperature of the fruit core, T_f, will equal the temperature of the surface. Therefore, $Q_e = \varepsilon \sigma T_f^4$ and $C = h_c (T_f - T_a)$. For forced convection about a sphere without the increased turbulence of the outdoor environment (Nobel 1975; Kowalski and

Mitchell 1976; Monteith (1973, page 224) give two formulae for the relationship between the Nusselt and the Reynolds number.

Range of Re	Nu
0-300	$2 + 0.54\ Re^{0.5}$
$50 - 1 \times 10^5$	$0.34\ Re^{0.6}$

Calculate Nu by both formulae for Re = 50, 100 and 300. If D = 1 cm, what is the minimum wind speed for which the second relationship is valid? Which formula yields a lower heat transfer coefficient? What will the effect on the energy balance of the fruit be? Find h_c as a function of D (0.01, 0.04 and 0.1 m) and V (0.1, 1.0 and 10.0 m s^{-1}) if Nu = $0.34\ Re^{0.6}$. Assume $\nu = 1.42 \times 10^{-5}\ m^2\ s^{-1}$ for the entire problem.

For a sphere: $Q_a = a_s\ [A_1S + A_2s + A_3r + (S+s)] + a_\ell A_\ell [R_a + r_g]$

where

a_s = the absorptivity to shortwave radiation (assume .7),

A_1 = the percent of the total surface hit by direct beam radiation weighted by the angle of incidence (equals $\pi r^2/4\pi r^2 = 1/4$)

S = direct beam solar radiation (W m^{-2}),

$A_2 = A_s = A_\ell$ = the percent of the total surface hit by the corresponding radiation sources (assume 0.5),

s = diffuse shortwave radiation (assume = 0.1 of total shortwave radiation R_p, W m^{-2})

r = reflectivity of the ground (assume 0.15),

a_ℓ = absorptivity to longwave radiation (assume 1.0),

R_a = longwave radiation from the atmosphere (W m^{-2}),

and

R_g = longwave radiation from the ground (W m^{-2}).

From Morhardt and Gates (1974, page 20, Fig. 2c), I have taken R_p, R_a and R_g for a sunny day and converted the units to W m^{-2} as tabulated below:

TABLE FOR PROBLEM 9b

Hour of the Day	R_p (W m^{-2})	R_a (W m^{-2})	R_g (W m^{-2})	T_a (^oC)
7	35	223	335	7.5
8	593	223	348	10.0
9	837	230	369	12.0
10	1012	237	419	15.0
11	1116	244	461	19.0
12	1186	251	502	24.0
13	1116	258	481	27.0
14	1012	251	461	25.0
15	837	244	419	22.0
16	593	237	391	16.0
17	35	237	363	12.5
18	0	230	349	10.0

Calculate Q_a values for each hour of the day. What part of this is shortwave radiation?

Assuming that the wind speed is 1.0 m/s and that the diameter of the fruit is 0.04 m and using the convection coefficient you have derived, calculate the fruit's equilibrium temperature for each hour of the day. Using Q_a and T_a values for 7 and 12 o'clock calculate the equilibrium fruit temperature for all combinations of V = 0.1, 1.0 and 10.0 m/s and D = 0.01, 0.04, 0.10 m. Size and wind speed affect the fruit temperature in opposite ways at the two times. Why is this? What are the problems with this approach?

10. Discuss the following group of papers concerning heat transfer in biology:

Strunk, T. H. 1971. Heat loss from a Newtonian animal. J. Theoret. Biol. 33:35-61.

Kleiber, M. 1972. A new Newton's Law of cooling? Science 178:1283-1285.

Tracy, C. R. 1972. Newton's Law: its applicability for expressing heat losses from homeotherms. BioScience 22:656-659.

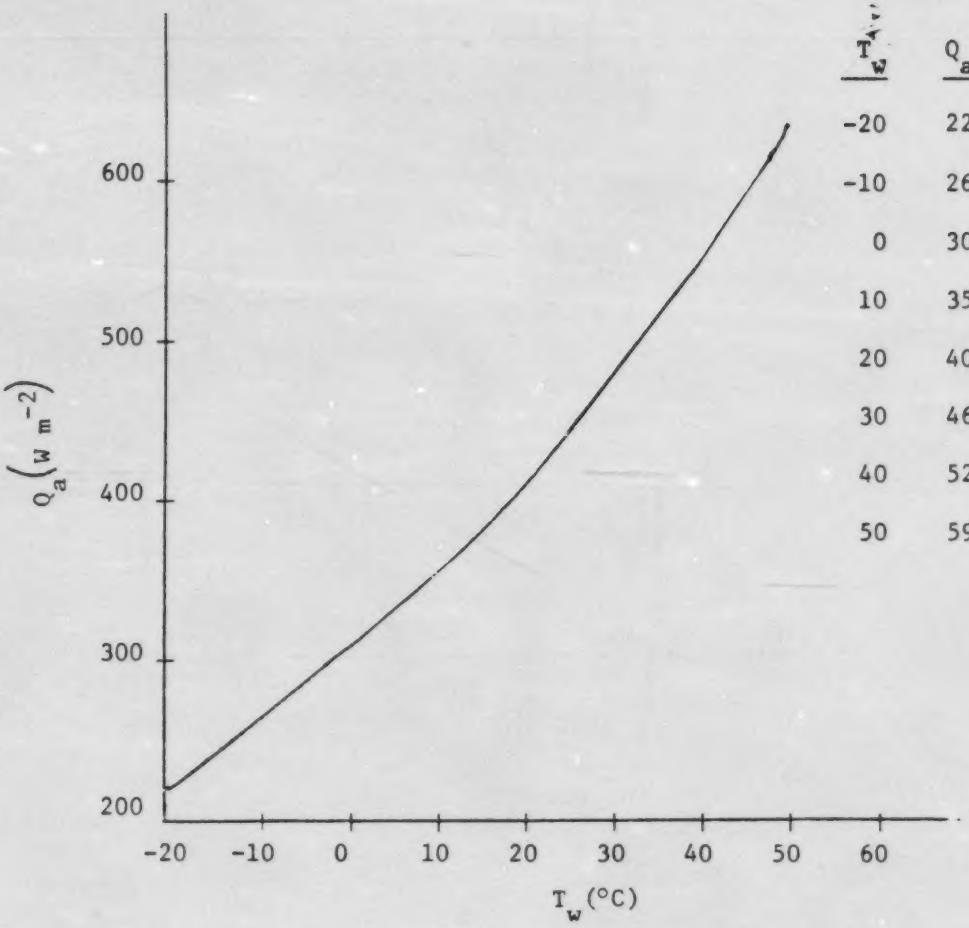
Technical Comments: Perspectives of linear heat transfer: T. H. Strunk, C. R. Tracy, M. Kleiber. Science 181:184-186.

Linearized heat transfer relations in biology. G. S. Bakken and D. M. Gates; T. H. Strunk; M. Keiber. Science 183:976-978.

Bakken, G. S., and D. M. Gates. 1974. Notes on "Heat loss from a Newtonian animal." J. Theoret. Biol. 45:283-292.

PROBLEM SOLUTIONS

1.



T_w	Q_a
-20	223.6
-10	261.0
0	303.3
10	350.1
20	402.2
30	460.0
40	523.8
50	593.6

1a. Metabolic heat will increase the wall temperature. The smaller the chamber, the greater this effect will be. The influence will change as the square of the distance.

b. The absorptivity is 0.96. Two ways to minimize wall heating are to make the chamber large relative to the animal or immerse the chamber in water. If the emissivity for the metal walled chamber is 0.15 absorptivity will be 0.15. Because the walls will not transmit longwave radiation, 85% will be reflected back to the animal and the other sides

of the chamber, again making the chamber feel warmer to the animal than the air or wall temperatures would indicate. Changing the inside surface characteristics of the chamber or increasing the chamber size relative to the animal will reduce the importance of reflected radiation. (*See* Porter 1969 and Morhardt and Gates 1974 for discussion.)

2a. $E_f = \lambda^{-2} E_\lambda / c_L$. The dimensions of E_f are $M L^{-2}$ and of E_λ are $M T^{-1} L^{-3}$. They differ by a factor of $L^{-1} T^{-1}$. If $\lambda f = c_L$ and $n = \lambda^{-1}$ then $n = f/c_L$. (For plots *see* data below and the following figures.) Because wavelength is inversely proportional to wave number, equal bandwidths on a wavelength plot will cause unequal bandwidths on a wave

Table for Problem 2.

T (K)	λ ($m \times 10^{-6}$)	n ($m^{-1} \times 10^{6}$)	f ($s^{-1} \times 10^{14}$)	E_λ ($J\ m^{-3} s^{-1}$)	E_f ($J\ m^{-2}$)
280	4.0	0.250	0.750	0.10×10^{7}	0.05×10^{-1}
	5.0	0.200	0.600	0.41	0.35
	6.0	0.167	0.500	0.92	1.10
	7.0	0.143	0.429	1.45	2.37
	8.0	0.125	0.375	1.86	3.98
	9.0	0.111	0.333	2.11	5.71
	10.0	0.100	0.300	2.21	7.38
	11.0	0.091	0.273	2.20	8.87
	12.0	0.083	0.250	2.11	10.31
	13.0	0.077	0.231	1.98	11.14
	15.0	0.067	0.200	1.66	12.45
	17.0	0.659	0.176	1.35	13.00
	20.0	0.050	0.150	0.97	12.95
	30.0	0.033	0.100	0.34	10.17
	40.0	0.025	0.075	0.14	7.46
	60.0	0.017	0.050	0.04	4.25
	100.0	0.010	0.030		1.85
	150.0	0.007	0.020		0.90
6000	0.15	6.66	20.00	0.06×10^{13}	$\times 10^{-8}$
	0.20	5.00	15.00	0.73	0.10
	0.25	4.00	12.00	2.63	0.55
	0.30	3.33	10.00	5.22	1.57
	0.35	2.86	8.57	7.57	3.09
	0.40	2.50	7.50	9.15	4.88
	0.45	2.22	6.67	9.91	6.69
	0.50	2.00	6.00	10.00	8.33
	0.55	1.82	5.46	9.65	9.73
	0.60	1.67	5.00	9.03	10.83
	0.65	1.54	4.62	8.28	11.66
	0.70	1.43	4.29	7.50	12.24
	0.80	1.25	3.75	6.01	12.81
	0.90	1.11	3.33	4.74	12.82
	1.00	1.00	3.00	3.75	12.48
	1.25	.80	2.40	2.11	11.00
	1.50	.67	2.00	1.25	9.37
	2.00	.50	1.50	.51	6.73
	3.00	.33	1.00	.13	3.77
	5.00	.20	.60	.02	1.62
	10.00	.10	.30		.46

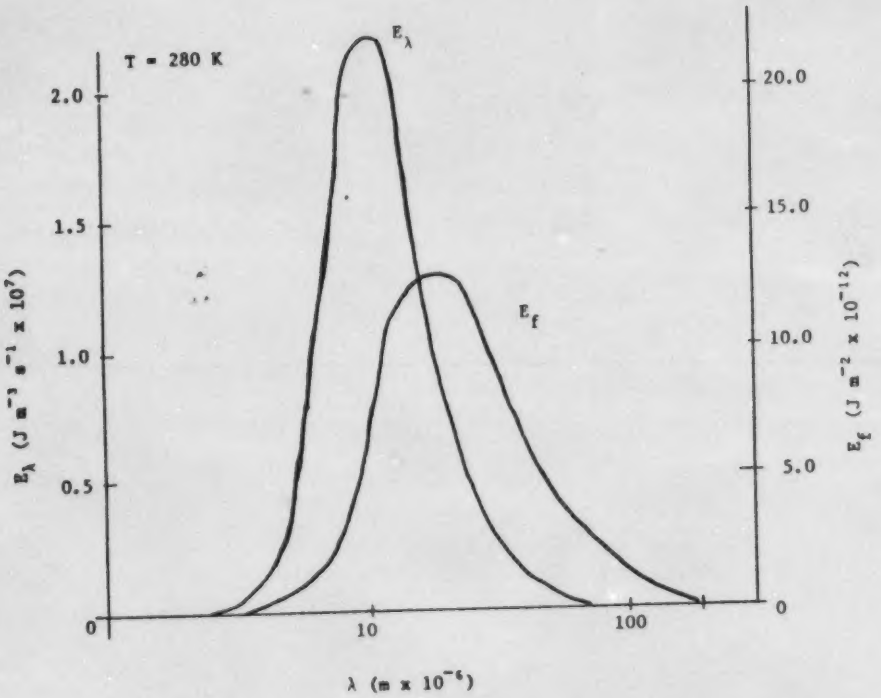


Figure for Problem 2. Emitted radiation as a function of temperature (T = 280 K).

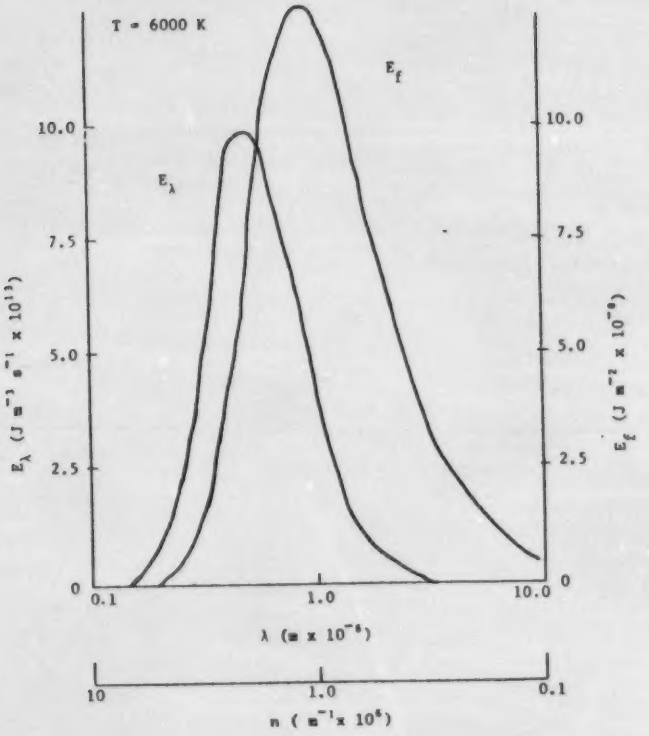


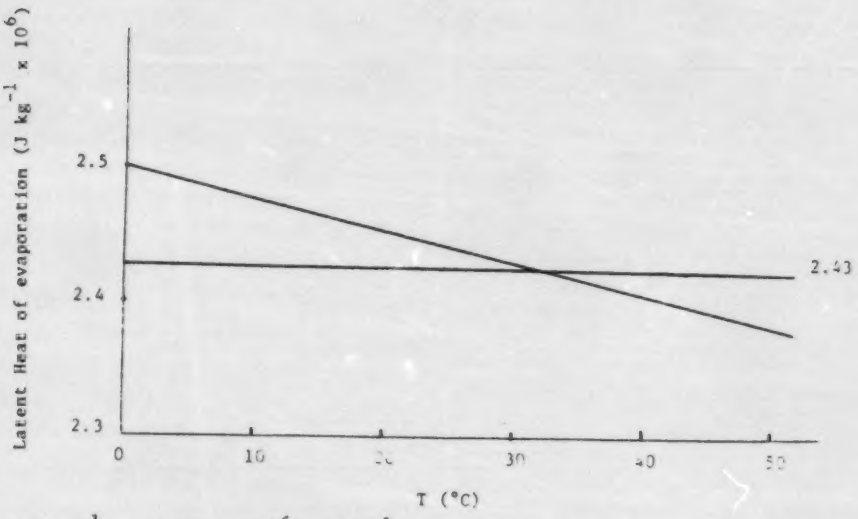
Figure for Problem 2a. Emitted radiation as a function of temperature (T = 6000 K).

number plot. For equal wavelength bandwidths larger wave numbers imply larger bandwidths.

b. A frequency or wave number plot has the property that equal areas represent equal amounts of energy which is not true of a wavelength plot. The maximum energy is at $\lambda \simeq 0.85 \times 10^{-6}$ m which is in the near infrared portion of the spectrum, while Fig. 4 shows $\lambda_{max} \simeq 0.48 \times 10^{-6}$ m.

3a. Equation (16) is

$$L(T) = 2.50 \times 10^{6} - 2.38 \times 10^{3} T$$



580 cal g^{-1} = 2.43 x 10^{6} J kg^{-1}.

Body temperature for most homeotherms is above 36 °C. Expelled air will be below body temperature so this seems like a good estimate. If the air was really at 0 °C, the error would be:

$$\frac{2.50 - 2.43}{2.43} = 2.9 \text{ percent.}$$

At 45 °C, the error would be:

$$\frac{2.43 - 2.40}{2.43} = 1.2 \text{ percent.}$$

b. For the moose

$$V_L = 0.0567\ (358)^{1.02} = 22.83\ \frac{\text{liters}}{\text{breath}}$$

Liters of air per min are:

$$R_v = 176.3 \exp\ (.07\ T_a),$$

$$R_v = 2.94 \exp\ (.07\ T_a)\ m^3 \times 10^{-3} s^{-1}.$$

Assume that the air is saturated at $T_b = 38\ ^oC$. We need to calculate the kg of water vapor in a liter of air (C_e, kg m^{-3}) exhaled at $(T_b + T_a)/2$

$$C_e = \frac{me(T)}{RT},$$

where

m is molecular weight of water (18 g mol^{-1}),

R is the gas constant (8.13 J $mol^{-1}K^{-1}$),

T is temperature (k at $\frac{T_b - T_a}{2}$),

and

e(T) is saturated vapor pressure of water at temperature (T) (mbars).

$$C_e = \frac{18\ g\ mol^{-1}\ e_s\ (T)}{8.31\ kg\ m^2 s^{-2} mol^{-1} K^{-1}\ T}$$

$$C_e = \frac{.217\ e\ \ (T_a + T_b)/2}{(T_b + T_a)/2}$$

The concentration of water vapor inhaled is

$$C_i = \left[\frac{.217\ e(T_a)}{T_a}\right] r.h.$$

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$$LE = 2.43\ J\ kg^{-1}\ (C_e - C_i) \cdot R_v$$

$$= 2.43\ r.h. \left(\frac{.217e[(T_a + T_b)/2]}{(T_b + T_a)/2} - \frac{.217e(T_a)r.h.}{T_a} \right) \times 2.94 \exp (.07\ T_a).$$

Table of evaporative water loss as a function of expelled temperature.

°C		kg m^{-3}					m^3 x 10^{-3} s^{-1}	W	
T_a	$\frac{T_a+T_b}{2}$	C_e	C'_e	C_i	(C_e-C_i)	$(C_e-C_i)'$	R_v	LE	LE'
-20	9	.0090	.001	.0005	.0085	.0005	.73	15	0.90
-10	14	.0120	.0024	.0012	.0108	.0012	1.45	38	4.2
0	19	.0164	.0048	.0024	.0140	.0024	2.94	100	17.1
10	24	.0218	.0096	.0048	.0170	.0048	5.92	244	69.1
20	29	.0290	.0172	.0086	.0204	.0086	11.92	591	249
30	34	.0375	.0302	.0151	.0224	.0151	24.01	1307	881
40	39	.0485	.0510	.0255	.0270	.0255	48.34	3172	2996

4. The conduction transfer during steady state can be calculated according to the following formula:

$$G = \frac{kA_c(T_b - T_g)}{\Delta x}$$

Table of G values (W)

T_g (°C) \ k(W m^{-1} °C^{-1})	.02	.08	.17
2	3.89	15.55	33.05
14	1.30	5.18	11.02
27	-1.51	-6.05	-12.85

5. By definition

$$q_1 = \frac{k_1}{L_1} (T_1 - T_B) \quad \text{and} \quad q_2 = \frac{k_2}{L_2} (T_B - T_2).$$

From the First Law of Thermodynamics, we know that

$$q_1 = q_2. \quad \text{Therefore,} \quad \frac{k_1}{L_1} (T_1 - T_B) = \frac{k_2}{L_2} (T_B - T_2).$$

Solving for T_B, we have

$$T_1\left(\frac{k_1}{L_1}\right) + T_2\left(\frac{k_2}{L_2}\right) = T_B\left(\frac{k_1}{L_1} + \frac{k_2}{L_2}\right)$$

$$T_B = T_1\left(\frac{L_2 k_1}{L_2 k_1 + L_1 k_2}\right) + T_2\left(\frac{L_1 k_2}{L_2 k_1 + L_1 k_2}\right)$$

let $k_1 = ak_2$ and $L_1 = bL_2$, then

$$T_B = T_1\left(\frac{L_2 a k_2}{L_2 a k_2 + b L_2 k_2}\right) + T_2\left(\frac{b L_2 k_2}{L_2 a k_2 + b L_2 k_2}\right)$$

$$T_B = \frac{L_2 k_2}{L_2 k_2}\left(\left(\frac{T_1\, a}{a + b}\right) + \left(\frac{T_2\, b}{a + b}\right)\right) = \frac{1}{a+b} (T_1 a + T_2 b).$$

Now let $\frac{a}{b} = x$

$$T_B = \frac{1}{x+1} (T_1 x + T_2).$$

Since $a > 1$, $k_1 > k_2$ so material 1 has the steeper temperature gradient. Because $x = \frac{a}{b} = \frac{1.2}{.2} = 6.0$, the total temperature drop is greater in material 2. $T_B = 35.7$ °C.

b. A more realistic description of the heat transfer would allow for a slight temperature drop in the soil. Then, in part a, $T_1 = T_g$ and $T_2 = T_b$.

c. The skin will warm from its initial temperature of 22 °C towards ground temperature. Because heat is leaving the soil there will be a thin layer that cools down from 30 °C. Eventually an equilibrium will be reached and the temperature profile will be constant.

6.

Re		
V / D	0.1	2.0
.46	3239	64789
1002	14	282

Nu	$Nu = a.Re^b$	
V / D	0.1	2.0
.46	26.59	178.51
.002	2.27	8.52

$$h_c = \frac{Nu\ k}{D}$$

V / D	0.1	2.0
.46	1.45	9.70
.002	28.38	106.5

7.

$$Nu = 0.60\ Re^{0.5}\ ,\ h_c = \frac{Nu\ k}{D}$$

$$h_c = \frac{k}{D}\ 0.60 \left[\frac{V\ D}{\nu}\right]^{0.5} = \frac{0.60}{(\nu)0.5} \times k \left[\frac{V}{D}\right]^{0.5}$$

$$h_c = 3.98 \left[\frac{V}{D}\right]^{0.5}$$

This is approximately 2.3 times the value of 9.14 J m^2 $^oC^{-1}$ $s^{-1/2}$ that Gates uses. Most wind speeds in natural environments are less than 3 m s^{-1} and most leaves are less than 0.1 m along their largest dimension, thus, Re < 20,000. Leaves usually will not flutter at wind speeds less than 3 m s^{-1}. (*See* figure for Problem 7 on following page.) *See* Grace (1977) for additional information.

Figure for Problem 7

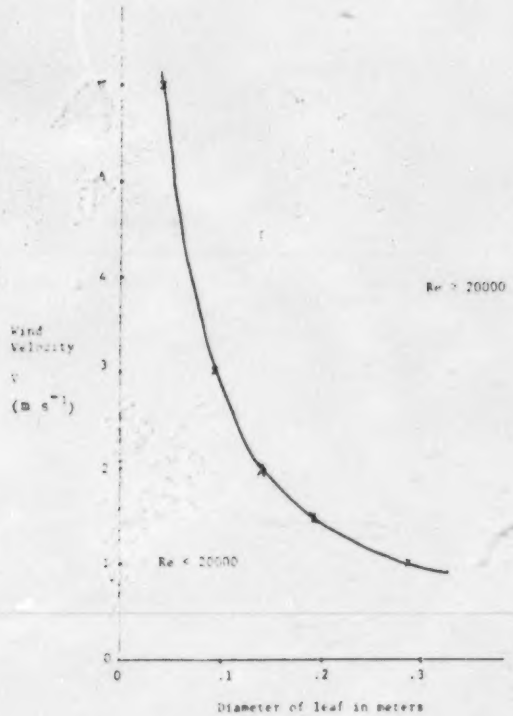
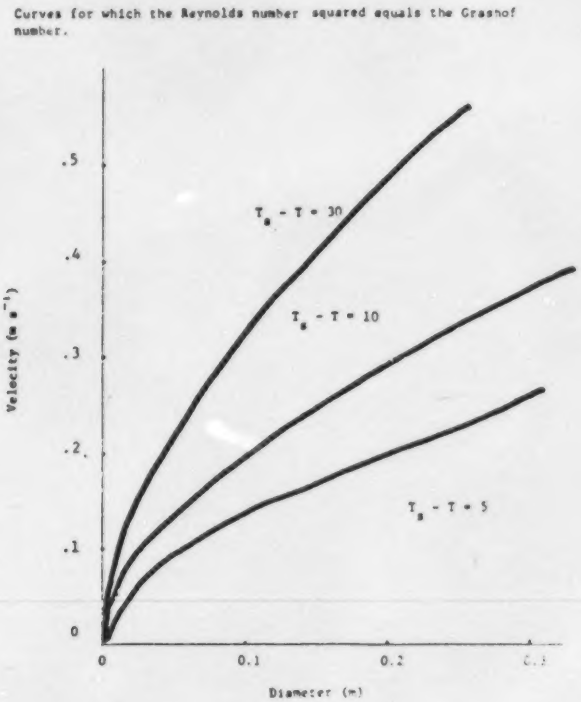


Figure for Problem 8



8. $Re^2 = Gr$

$$Re^2 = Gr$$

$$\frac{D^2V^2}{\nu^2} = \frac{ag\,D^3(T_s - T)}{\nu^2}$$

$$V^2 = ag\,D(T_s - T)$$

$$V = .1895\sqrt{(T_s - T)D}$$

Velocity (m 5^{-1}) as a function of T_s - T and D

	T_s - T (°C)		
D (m)	5	10	20
.3	.232	.328	.568
.2	.189	.268	.464
.1	.134	.189	.328
.05	.095	.134	.232
.01	.042	.060	.104

From Figures 10, 11, and 12 in the text it is clear that leaf temperature is usually not more than 10 °C above air temperature (although this is a function of leaf size in Fig. 12). Leaf size is usually less than .05 m and wind speed is below 3 m s^{-1}. There still remains a set of conditions where free convection may be important. For additional information see Tibbals et al. (1964) and Grace (1977).

9a. The degree days DD = 30. This approach assumes: 1) that the high and low air temperatures will represent the average thermal conditions that the fruit experiences; 2) that development is a linear function of the high and low average; and 3) that there is no problem with the fruit overheating. There are undoubtedly other problems also.

b. For Re = 50 and D = 0.01 m, 1.42×10^{-5}

$$Re = \frac{DV}{\nu} \cdot \text{ So } V = \frac{Re\ \nu}{D} = \frac{50 \times 1.42 \times 10^{-5}}{0.01} = .710 \text{ m/s}$$

A comparison of the Nusselt numbers at the same Reynolds number (in the range 50-300) shows that the Nusselt number computed by the first formula is larger. Since the heat transfer coefficient is proportional

to the Nusselt number, the choice of the second formula will give a lower convection coefficient. Choosing the second formula will make the fruit's temperature depart from air temperature to a greater extent than the first formula.

$$Re = \frac{DV}{\nu} \quad so \quad Nu = 0.34 \left(\frac{DV}{\nu}\right)^{0.6} \quad and \quad h_c = \frac{0.34 \left(\frac{DV}{\nu}\right)^{0.6} k}{D}.$$

Therefore, if

$$k = 0.025 \text{ W m}^{-1} \text{ K}^{-1}, \quad h_c = 6.8 \, V^{0.6} \, D^{-0.4}.$$

h_c for a sphere

	V(m/s)		
D(m)	0.1	1.0	10.0
0.01	10.8	42.9	170.8
0.04	6.2	24.6	98.1
0.1	4.3	17.1	68.0

Q_a values are in the table below. Because a_s, A_1, A_2, A_3, r and S/s are assumed constant, the absorbed shortwave radiation is equal to 0.245 R_p.

Time (hours)	7	8	9	10	11	12	13	14	15	16	17	18
Q_a (kWm^{-2})	288	431	505	576	626	667	642	604	536	459	308	292
T_a (°C)	7.5	10.0	12.0	15.0	19.0	24.0	27	25	22	16	12.5	10
T_f (°C)	6.0	12.9	17.0	21.9	26.8	32.1	33.7	30.9	26.2	18.8	10.8	8.1

For 7 o'clock

T_f values (°C)

	V(m/s)		
D(m)	0.1	1.0	10.0
0.01	4.6	6.6	7.2
0.04	3.3	6.0	7.1
0.1	2.4	5.4	6.9

For 12 o'clock

T_f values (°C)

	V(m/s)		
D(m)	0.1	1.0	10.0
0.01	38.7	29.1	25.4
0.04	43.9	32.1	26.4
0.1	47.3	34.8	27.4

The T_f values given can be more accurately computed for the conditions given but the estimates of R_p, R_a, R_g and T_a do not warrant it. If the absorbed radiation is below that found in a blackbody cavity at air temperature T_a, then decreasing the convection coefficient (decrease V or increase D) will increase the difference between T_a and T_f making the fruit colder. Conversely if Q_a is greater than a blackbody level increasing the convection coefficient will bring the fruit closer to air temperature. The problems with this approach are several. Usually the radiation fluxes are much more complex than we have considered because of surrounding vegetation or other fruit. Clumping of fruits will also decrease the convection coefficient. The microclimate on opposite sides of a plant is often different and difficult to specify accurately in small places.

The fruits grow and change color during the season. Smart and Sinclair (1976) have investigated some of these problems as well as the temperature differences within one fruit and nonsteady state conditions.

10. No solution provided.

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APPENDIX I. Symbols, Units and Dimensions

Symbol	Quantity	Unit	Dimensio
A_c	Area in contact with substrate	m^2	L^2
A_e	Area of emittance	m^2	L^2
A_i	Percent of total surface area exposed to radiation source i	--	--
a	Constant	--	--
a(λ)	Absorptivity at wavelength λ	--	--
a_ℓ	Average absorptivity to longwave radiation	--	--
a_s	Average absorptivity to shortwave radiation	--	--
Br	Breathing rate	min^{-1}	T^{-1}
b	Constant	--	--
C	Convection	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
C	Heat capacity	$J\ °C^{-1}$	$H\ \Theta^{-1}$
c	Specific heat	$J\ kg^{-1}\ °C^{-1}$	$H\ M^{-1}\ \Theta^{-1}$
C_a	Water vapor concentration of the air	$kg\ m^{-1}$	$M\ L^{-1}$
C_e	Water vapor concentration of exhaled air	$kg\ m^{-1}$	$M\ L^{-1}$

APPENDIX I. Symbols, Units and Dimensions (continued)

Symbol	Quantity	Unit	Dimension
c_L	Speed of light 3×10^8	$m\ s^{-1}$	$L\ T^{-1}$
C_o	Water vapor concentration at the surface of the organism	$kg\ m^{-1}$	$M\ L^{-1}$
c_v	Volumetric specific heat	$J\ m^{-3}\ °C^{-1}$	$H\ L^{-3}\ \Theta^{-1}$
c_1	Constant = $2\pi hc_L^2$	--	--
c_2	Constant = $hc_L\ K_b^{-1}$	--	--
D	Characteristic length	m	L
DD	Degree days	°C day	$\Theta\ T$
E	Evaporation	$kg\ s^{-1}$	$M\ T^{-1}$
E_f	Radiation flux per unit frequency	$J\ m^{-2}$	$H\ L^{-2}$
E_λ	Radiation flux per unit wavelength	$J\ m^{-3}\ s^{-1}$	$H\ L^{-3}\ T^{-1}$
e	Vapor pressure	$kg\ m^{-1}\ s^{-2}$	$M\ L^{-1}\ T^{-2}$
e	Energy in a photon	J	H
f	Frequency	s^{-1}	T^{-1}
G	Conduction	W	$H\ T^{-1}$
g	Acceleration of gravity	$m\ s^{-2}$	$L\ T^{-2}$
Gr	Grashof number	--	--

APPENDIX I. Symbols, Units and Dimensions (continued)

Symbol	Quantity	Unit	Dimension
h_c	Convection coefficient	$W\ K^{-1}$	$H\ T^{-1}\ \Theta^{-1}$
h	Planck's constant	6.63×10^{-34} J s	H T
k	Thermal conductivity	$W\ m^{-1}\ °C^{-1}$	$H\ L^{-1}\ \Theta^{-1}\ T^{-1}$
K_b	Boltzmann's constant	$1.38 \times 10^{-23}\ J\ K^{-1}$	$H\ \Theta^{-1}$
K_g	Thermal conductance	$W\ °C^{-1}$	$H\ \Theta^{-1}\ T^{-1}$
k_1	Constant for leaf convection	$9.14\ J\ m^{-2}\ °C^{-1}\ S^{-\frac{1}{2}}$	$H\ L^{-2}\ \Theta^{-1}\ T^{-\frac{1}{2}}$
k_2	Constant for evaporation flux in leaf	$183\ S^{-\frac{1}{2}}\ m^{-1}$	$T^{-\frac{1}{2}}\ L^{-1}$
L	Latent heat of evaporation	$J\ kg^{-1}$	$H\ M^{-1}$
L_1	Length	m	L
L_2	Length	m	L
M	Mass	kg	M
M	Metabolism	$W\ m^{-2}$	$H^{-1}\ L^{-2}\ T^{-1}$
m	Molecular weight	$g\ mole^{-1}$	M
Nu	Nusselt number	--	--
n	Wave number	m^{-1}	L^{-1}
Q	Heat energy	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$

APPENDIX I. Symbols, Units and Dimensions (continued)

Symbol	Quantity	Unit	Dimension
Q_a	Absorbed radiation	W	$H\ T^{-1}$
Q_e	Emitted radiation	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
R	Gas constant	$J\ mol^{-1}\ K^{-1}$	Θ^{-1}
R_a	Atmospheric radiation (longwave)	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
R_g	Ground radiation (longwave)	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
R_p	Shortwave radiation from the sun and sky	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
R_v	Respiration rate	$m^3\ s^{-1}$	$L^3\ T^{-1}$
Re	Reynolds number	--	--
r.h.	Relative humidity	--	--
r	Resistance	$W^{-1}\ m^2\ °C$	$H^{-1}\ L^2\ T\ \Theta$
r	Reflectivity of the underlying surface	--	--
r_e	Resistance to water vapor loss	$s\ m^{-1}$	$T\ L^{-1}$
r_ℓ	Internal resistance of leaf	$s\ m^{-1}$	$T\ L^{-1}$
$r(\lambda)$	Reflectivity at wavelength λ	--	--
S	Shortwave radiation from the sun	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$
s	Shortwave radiation from the sky	$W\ m^{-2}$	$H\ L^{-2}\ T^{-1}$

APPENDIX I. Symbols, Units and Dimensions (continued)

Symbol	Quantity	Unit	Dimension
T	Temperature	°C	Θ
T_B	Boundary temperature	°C	Θ
T_a	Air temperature	°C	Θ
T_{amax}	Maximum daily air temperature	°C	Θ
T_{amin}	Minimum daily air temperature	°C	Θ
T_b	Body temperature	°C	Θ
T_f	Fruit temperature	°C	Θ
T_g	Ground temperature	°C	Θ
T_ℓ	Leaf temperature	°C	Θ
T_s	Surface temperature	°C	Θ
T_t	Threshold temperature	°C	Θ
T_w	Wall temperature	°C	Θ
t	Time	s	T
$t(\lambda)$	Transmittance at wavelength λ	--	--
U	Internal energy	J	H
V	Fluid velocity	$m\ s^{-1}$	$L\ T^{-1}$
V	Volume	m^3	L^3

APPENDIX I. Symbols, Units and Dimensions (continued)

Symbol	Quantity	Unit	Dimension
V_L	Volume of the lungs	m^3	L^3
W	Leaf dimension transverse to the wind	m	L
x	Boundary layer thickness	m	L
z	Depth	m	L
ε	Emittance	--	--
κ	Thermal diffusivity	$m^2\ s^{-1}$	$L^2\ T^{-1}$
λ	Wavelength	m	L
λ_{max}	Wavelength of maximum radiation	m	L
ν	Kinematic viscosity	$m^2\ s^{-1}$	$L^2\ T^{-1}$
ρ	Density	$kg\ m^{-3}$	$M\ L^{-3}$
σ	Stefan-Boltzmann constant	$5.67 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$	$H\ L^{-2}\ T^{-1}\ \Theta^{-}$
μ	Fluid viscosity	$kg\ m^{-1}\ s^{-1}$	$M\ L\ T^{-1}$

M = Mass

L = Length

T = Time

Θ = Temperature

$H = M\ L^2\ T^{-2}$